FIFTY YEARS OF DARWINISM

MODERN ASPECTS OF EVOLUTION

CENTENNIAL ADDRESSES IN HONOR OF CHARLES DARWIN

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CONTENTS

PLATES

INTRODUCTION

BY

T. C. CHAMBERLIN

The greatness of a man is shown in what he is, in what he does, and in what he sets a-doing.

If the long list of contributions to the sessions of this Association for these fifty years were searched for products of thought whose stimulus sprang from the life and works of Charles Darwin, it would reveal an impressive testimonial to his greatness as a power in our scientific world. If it were possible to give such an intellectual product a material embodiment and an appropriate form, we could raise no more sincere monument to his memory. Even in the less tangible form it inevitably bears, it *is* our monument. By responses, individual and collective, to the marvelous suggestiveness of Darwin's inquiries and interpretations, the members of this Association during the last half century have been paying their truest tributes. More or less unconsciously, no doubt, but none the less genuinely, we have thus been doing honor to one of the greatest of intellectual leaders.

The magnitude of any moving force is measured scarcely less by the obstacles surmounted

and by the inertia overcome than by the positive momentum it generates. In the first decades of the great Darwinian movement in biology, the tribute of our members may not have been wanting in demonstrations of the force of old adhesions, but even then, whether by resistance or by coöperation, we gave our testimony to the new power that made itself felt in the scientific world. A little later we paid the tribute of conviction—the general tribute of willing conviction, on the part of some of us, and the even more significant tribute of reluctant conviction, on the part of others; but, in one way or another, we paid a universal tribute.

If we of the older school permit ourselves to be reminiscent, the tides of thought and feeling of the early days of the half century we celebrate easily surge back into consciousness. We readily recall the stirrings in the biological field when the great question of derivation of species arose into a concrete and, as it seemed to some, a threatening form. But it was not among us as biologists, but among us as members of a proud race, that emotion was deepest stirred. It was in the humanistic atmosphere that protests were most vibrant, for man—scientific man not excepted—is first of all a creature who takes thought of himself. His anthropic pride, fostered by traditional assumptions of separateness and eminent superiority—assumptions peculiar to no race, nation, or religion, but the common inheritance

of us all—rose up in remonstrance and put barriers in the way of a candid reception of the new interpretations. But still, with all his foibles, man, at least man of the better sort, proclaims adhesion to the ancient admonition, " Know thyself," and ultimately he strives to be loyal to the intellectual precedence he assigns himself. It is his to know the truth. Those of scientific trend early found occasion to call into fresh activity the maxim that it is better to accept the truth than to think of ourselves more highly than we ought to think. Whatever rufflings of our fond sense of humanistic caste were felt from the new interpretations in those first days of disturbed equanimity, we soon came to find complacency in the new place assigned us at the head of a multitudinous kin, the place of leadership in the van of a great procession of ascending tribes striving for supreme fitness.

But the days of disturbed tranquillity, for us of the scientific household at least, soon passed away; and, if they linger with any still, it can only be among those outside the wide limits of this Association. We are yet far from knowing the whole truth, but we are tranquil in the search for it, welcome or unwelcome as it may prove at first to be.

In the later decades of this memorable half century, the tribute of our membership, individual and collective, has lain in attempts to extend, to amend, to qualify, and to apply the

parent thought to which Darwin gave such prodigious impetus. To what result we have labored to add to, or to subtract from, his great conception, the future must decide. The *effort* is our tribute to the power that has moved us.

The biological realm was indeed the center of the great movement. Of this central movement and of the varied lines into which it has deployed, we shall learn through the words of those who are entitled to speak. To these, in a moment, I shall give place. But, though the revolution had its origin in the biological field, it was by no means limited to it. It soon became a radiant influence so penetrating and so stimulating that it has been felt in every field of thought. No realm of the intellectual world has failed to respond to the power of Darwin's method, the candor of his spirit, and the force of his clear insight and restrained judgment.

Darwin not only gave form to the whole trend of evolutionary inquiry, but he chastened and refined the moral aspects of thought in all lines of serious intellectual endeavor. It would be too much to say that he was the father of the evolutionary conception or the sole parent of the chastened moral attitude of thought now felt to be binding in the scientific world. We would do him a dishonor most obnoxious to his candid and truthful spirit if we were to assign him more than historic truth amply warrants. We must not fail to recognize that before his time the evolu-

tionary conception had found place in the thought of not a few philosophic inquirers, not the least among whom was one of his own lineage; but yet it was Charles Darwin, more than any other, who gave definiteness and concreteness, who gave method and spirit, to the doctrine of derivation, and who thus became parental to the great movement in a sense equaled by no other. Such acceptances of evolutionary conceptions as had much currency before his day, or had much tangible influence on research, were cosmogonic rather than biologic. Beyond doubt these pioneer gropings in the less biased fields prepared the way for his great contribution, but they did not equally encounter the central obstacle that lay in inherited adhesions and traditional prepossessions, and they did not, therefore, and could not, equally revolutionize the spirit and the attitude of the thinking world by touching with transforming power the mainspring of bias.

But if Darwin found some measure of preparation for his work in the labors of predecessors in his own and other fields, he more than amply repaid the debt. The stimulative influence of Darwinism on fundamental conceptions in the celestial and terrestrial kingdoms followed close on those in the biological realm. Both terrestrial and celestial history are even now in the flux of reinterpretation. The sources of this revision of view are indeed various, but a profound Darwinian influence is felt in it all. It would have

been felt had Darwin left nothing but his *Origin of Species* and the remarkable treatises that followed it, but he has added thereto leaders of thought of his own name and lineage, and they have carried his spirit and his breadth of view into realms he could not himself enter. The evolution of the earth and of the heavens has thus felt his transmitted touch. The concept of kinship of worlds follows easily on the concept of the kinship of organic beings.

In the transformed attitude of the intellectual world to-day, the mooted question of the hour—the evolution of the atom—finds a fair field, wherein evidence needs but to accredit itself duly to have its place and weight freely accorded it. If the atom shall show an authenticated pedigree, it will easily take its place in the procession of the derived, with the plant, the animal, the earth, and the stars.

The contributions of Darwin to the science which it has fallen to me to follow have been great and various, but the greatest of them all relate to the history of life on the globe. The geological record, as known in his day, was at once a foundation for his work and an obstacle to its acceptance. It was the mission of his interpretations to bring forth the added truth which made the foundation broader and firmer, and which not only removed the seeming obstacles in the evolutionary path, but replaced them by cogent evi-

dence of the continuity of life and of its successive steps of progress.

But it does not fall to me to enter upon any of the special fields to which Darwin made his monumental contributions. Your committee has wisely assigned the leading aspects of the theory of evolution to those peculiarly fitted to treat them by reason of their own high attainments. In this introductory word on behalf of the Association, I have found no more fitting way to express our appreciation than to recall the tribute we have been paying by what we have done, and what we are trying to do, because Darwin set us a-doing.

FIFTY YEARS OF DARWINISM

BY

EDWARD B. POULTON

On this historic occasion it is of special interest to reflect for a few moments on the part played by the New World in the origin and growth of the great intellectual force which dominates the past half century. The central doctrine of evolution, quite apart from any explanation of it, was first forced upon Darwin's mind by his South American observations during the voyage of the *Beagle;* and we may be sure that his experience in this same country, teeming with innumerable and varied forms of life, confirmed and deepened his convictions as to the importance of adaptation and thus prepared the way for Natural Selection. Wallace, too, at first traveled in South America; only later in the parts of the Old World tropics which stand next to South America in richness.

Asa Gray in the New World represented Sir Joseph Hooker in the Old, as regards the help given to Darwin before the appearance of the *Origin,* and in strenuous and most efficient defense after its appearance. Chauncey Wright similarly represents Henry Fawcett. Fritz Müller not only actively defended Darwin, but

continually assisted him by the most admirable and original observations carried out at his Brazilian home. Turning to those who in some important respects differed from Darwin, I do not think a finer example of chivalrous controversy can be found than that carried on between him and Hyatt. The immense growth of evolutionary teaching, in which John Fiske played so important a part, although associated with the name of Herbert Spencer, must not be neglected on an occasion devoted to the memory of Darwin.

Outside the conflict which raged around the *Origin,* we find Dana, the only naturalist who at first supported Darwin in his views on the persistence of ocean basins and continental areas, and Alexander Agassiz, for many years the principal defender of the Darwinian theory of coral islands and atolls.

American paleontology, famed throughout the world, has exercised a profound influence on the growth and direction of evolutionary thought. The scale and perfection of its splendid fossil records have attracted the services of a large band of the most eminent and successful laborers, of whom I can only mention the leaders:—Leidy, Cope, Marsh, Osborn, and Scott in the Vertebrata; Hall, Hyatt, and Walcott in the Invertebrate sub-kingdom. The study of American paleontology was at first believed to support a Neo-Lamarckian view of evolution, but this, as well as the hypothesis of polyphyletic origins,

was undermined by the teachings of Weismann. Difficulties for which the Lamarckian theory had been invoked were met by the hypothesis of Organic Selection suggested by Baldwin and Osborn, and in England by Lloyd Morgan. Weismann's contention that inherent characters are alone transmissible by heredity has also received strong support from the immense body of cytological, Mendelian, and mutationist work to which the present volume bears such eloquent testimony. Finally, the flourishing school of American psychology, under the leadership of William James and James Mark Baldwin, accepts, and in accepting helps to confirm, the theory of Natural Selection.

ERASMUS DARWIN AND LAMARCK

Professor Henry F. Osborn, in his interesting work *From the Greeks to Darwin,* concludes that Lamarck was unaware of Erasmus Darwin's *Zoonomia,* and that the parallelism of thought is a coincidence.[1] The following passage from a letter[2] written to Huxley probably in 1859, and published since the appearance of Professor Osborn's book, indicates that Charles Darwin suspected the French naturalist of borrowing from his grandfather:—

[1] *From the Greeks to Darwin,* New York, 1894, pp. 152-55. Professor Osborn shows that on p. 145 Erasmus Darwin made use of the term "acquired" in the sense of "acquired characters"; "changement acquis" is the form employed by Lamarck.

[2] *More Letters of Charles Darwin,* I, p. 125.

" The history of error is quite unimportant, but it is curious to observe how exactly and accurately my grandfather (in *Zoonomia*, Vol. I, p. 504, 1794) gives Lamarck's theory. I will quote one sentence. Speaking of birds' beaks, he says: ' All which seem to have been gradually produced during many generations by the perpetual endeavor of the creatures to supply the want of food, and to have been delivered to their posterity with constant improvement of them for the purposes required.' Lamarck published *Hist. Zoolog.* in 1809. The *Zoonomia* was translated into many languages."

A careful comparison of the French translation of the *Zoonomia* with Lamarck's *Philosophie Zoologique* and with a preliminary statement of his views published in 1802, would probably decide this interesting question.

THE INFLUENCE OF LYELL UPON CHARLES DARWIN

The limits of space compel me to pass by the youth of Charles Darwin, with the influence of school, Edinburgh and Cambridge, including the intimacy with Henslow and Sedgwick—friendships leading to his voyage in the *Beagle,* an event which more than any other determined his whole career. We must also pass by his earliest convictions on evolution, the first note-book begun in 1837, the reading of Malthus and discovery of Natural Selection in October, 1838, the imperfect sketch of 1842, the completed sketch of 1844.

It is necessary, however, to pause for a brief consideration of the influence of Sir Charles

Lyell. Although the writings of the illustrious geologist have always been looked upon as among the chief of the forces brought to bear upon the mind of Darwin, evidence derived from the later volumes of correspondence justifies the belief that the effect was even greater and more significant than has been supposed.

Huxley has maintained with great force that the way was paved for Darwin by Lyell's *Principles of Geology* far more thoroughly than by any other work.

> " . . . Consistent uniformitarianism postulates evolution as much in the organic as in the inorganic world. The origin of a new species by other than ordinary agencies would be a vastly greater 'catastrophe' than any of those which Lyell successfully eliminated from sober geological speculation."[1]

When the *Principles* first appeared Darwin was advised by Henslow to obtain and study the first volume, "but on no account to accept the views therein advocated." But a study of the very first place at which the *Beagle* touched, St. Iago, one of the Cape de Verde Islands, showed Darwin the infinite superiority of Lyell's teachings. He wrote to L. Horner,[2] August 29, 1844:—

> "I have been lately reading with care A. d'Orbigny's work on South America, and I cannot say how forcibly impressed I am with the infinite superiority of the Lyellian school of Geology over the continental. I

[1] *Life and Letters of Charles Darwin*, II, p. 190.
[2] *More Letters*, II, p. 117.

always feel as if my books came half out of Lyell's brain, and that I never acknowledge this sufficiently; nor do I know how I can without saying so in so many words— for I have always thought that the great merit of the *Principles* was that it altered the whole tone of one's mind, and therefore that, when seeing a thing never seen by Lyell, one yet saw it partially through his eyes —it would have been in some respects better if I had done this less, . . . "

This letter was written a few weeks after the date, July 5, 1844, which marks the completion of the finished sketch of that year. On July 5 Darwin wrote the letter to his wife begging her, in the event of his death, to arrange for the publication of the account he had just prepared. At this psychological moment in his career he wrote of the influence received from Lyell, and we are naturally led to observe how essentially Lyellian are the three lines of argument—two based on geographical distribution, one on the relation between the living and the dead—which first led Darwin toward a belief in evolution! The thoughts which shook the world arose in a mind whose whole tone had been altered by Lyell's teachings. Inasmuch as the founder of modern geology received his first inspiration from Buckland, Oxford may claim some share in moulding the mind of Darwin.

"COMING EVENTS CAST THEIR SHADOWS BEFORE"

The characteristic feature in which Natural Selection differs from every other attempt to

solve the problem of evolution is the account taken of the struggle for existence, and the rôle assigned to it. This struggle is keenly appreciated in Tennyson's noble poem, *In Memoriam,* the dedication of which is dated 1849, ten years before the *Origin.* The poet is disquieted by:—

> "Nature red in tooth and claw
> With ravine, . . ."

and by

> ". . . finding that of fifty seeds
> She often brings but one to bear."

It is interesting to note that the obvious understatement of this last passage is corrected in the author's notes published by his son a few years ago. In these we find "for fifty" read "myriad." The poignant sense of the waste of individual lives is brought into close relation in the poem with the destruction of the type or species:—

> "So careful of the type she seems,
> So careless of the single life;
>
> . . . . .
>
> 'So careful of the type'? but no,
> From scarpèd cliff and quarried stone
> She cries 'A thousand types are gone:
> I care for nothing, all shall go.'"

In this association between the struggle for existence waged by individuals and the extinction and succession of species we seem to approach the central idea of Darwin and Wallace. I asked Dr. Grove of Newport in the Isle of Wight if he

would point out the parallelism, so far as it existed, to his illustrious patient, hoping that some light might be thrown on the source of the inspiration. Nor was I disappointed. "Stay," said the aged poet when Dr. Grove had spoken, "*In Memoriam* was published long before the *Origin of Species.*" "Oh! Then you are the man," replied the doctor. "Yes, I am the man." There was silence for a time and then Tennyson said: "I don't want you to go away with a wrong impression. The fact is that long before Darwin's work appeared these ideas were known and talked about." From this deeply interesting conversation I think it is probable that, through mutual friends, some echo of Darwin's researches and thoughts had reached the great author of *In Memoriam.*

The light which has been recently thrown [1] upon Philip Gosse's remarkable book, *Omphalos,* indicates that its appearance in 1858 was connected with the thoughts that were to arouse the world in the following year. The author of *Omphalos* was a keen and enthusiastic naturalist held fast in the grip of the narrowest of religious creeds. We learn with great interest that he and others were by Lyell's advice prepared beforehand for the central thoughts of the *Origin.* To the new teaching all the naturalist side of his nature responded, but from it the religious side recoiled. Religion conquered in the strife, but the natural-

[1] In *Father and Son*, London, 1907.

ist found comfort in the perfectly logical conclusion that:—

> "Any breach in the circular course of nature could be conceived only on the supposition that the object created bore false witness to past processes, which had never taken place." [1]

Thus the divergence between the literal interpretation of Scripture and the conclusions of both geologist and evolutionist were for this remarkable man reconciled by the conviction:—

> "That there had been no gradual modification of the surface of the earth, or slow development of organic forms, but that when the catastrophic act of creation took place, the world presented, instantly, the structural appearance of a planet on which life had long existed." [2]

Philip Gosse could not but believe that the thoughts which had brought so much comfort to himself would prove a blessing to others also. He offered *Omphalos* "with a glowing gesture, to atheists and Christians alike. . . . But, alas! atheists and Christians alike looked at it and laughed, and threw it away." [3] Charles Kingsley expressed the objection felt by the Christian when he wrote that he could not "believe that God had written on the rock one enormous and superfluous lie." [4]

About twenty years ago I was present when precisely the same conclusion was advanced by a high dignitary of the English Church. He argued that even if the history of the Universe

[1] *Father and Son*, pp. 120, 121.
[2] *L. c.*, p. 120.
[3] *L. c.*, p. 122.
[4] *Ibid.*

were carried back to a single element such as hydrogen, the human mind would remain unsatisfied and would inquire whence the hydrogen came, and that any and every underlying form of matter must leave the inexorable question "whence?" still unanswered. Therefore if in the end the question must be given up, we may as well, he argued, admit the mystery of creation in the later stages as in the earlier. Thus he arrived at the belief in a world formed instantaneously, ready-made and complete, with its fossils, marks of denudation, and evidences of evolution—a going concern. Aubrey Moore, the clergyman who more than any other man was responsible for breaking down the antagonism toward evolution then widely felt in the English Church, replied very much as Kingsley had done, that he was unwilling to believe that the Creator had deliberately cheated the intellectual powers He had made. I may add that, inasmuch as science consists in the attempt to carry down causation as far as possible, it is above all the scientific side of the human intellect that is outraged,—no weaker term can be used,—by this more modern development of the argument of *Omphalos*.

THE PUBLICATION OF THE DARWIN-WALLACE ESSAY

In May, 1856, Darwin, urged by Lyell, began to prepare for publication. He had determined

to present his conclusions in a volume, for he was unwilling to place any responsibility for his opinions on the council of a scientific society. On this point he was, as he told Sir Joseph Hooker, in the only fit state for asking advice; namely, with his mind firmly made up: then *good* advice was very comforting while it was perfectly easy to reject *bad* advice. The work was continued steadily until June 18, 1858, when Wallace's letter and essay arrived from Ternate. As a result of the anniversary held in London on July 1 last year new light has been thrown upon the circumstances under which the joint essay was published fifty years before.

In consequence of the death of the eminent botanist, Robert Brown, Vice-President and ex-President of the Linnean Society, the last meeting of the summer session, called for June 17, was adjourned. The by-laws required that the vacancy on the Council should be filled up within three months, and a special meeting was called for July 1, for this purpose. Darwin received Wallace's essay on June 18, too late for the summer meetings of the Society, but in good time for Lyell and Hooker to present it to the special meeting. Hence, as Sir Joseph Hooker said on July 1st last, the death of Robert Brown caused the theory of Natural Selection to be " given to the world at least four months earlier than would otherwise have been the case." Sir Joseph Hooker also informed us that from June 18 up

to the evening of July 1, when he met Sir Charles Lyell at the Society, all the intercourse with Darwin and with each other was conducted by letter, and that no fourth person was admitted into their confidence. The joint essay was read by the secretary of the Society. Darwin was not present, but both Lyell and Hooker " said a few words to emphasize the importance of the subject." Among those who were present were Oliver, Fitton, Carpenter, Henfrey, Burchell, and Bentham, who was elected on the Council and nominated as Vice-President in place of Robert Brown. I cannot resist the temptation to reprint from the memorial volume issued by the Linnean Society of London some passages in the address which A. R. Wallace felt constrained to deliver on July 1, 1908, protesting against the too great credit which he believed had been assigned to himself. After describing Darwin's discovery of Natural Selection and the twenty years devoted to confirmation and patient research, Wallace continued:—

" How different from this long study and preparation —this philosophic caution—this determination not to make known his fruitful conception till he could back it up by overwhelming proofs—was my own conduct. The idea came to me, as it had come to Darwin, in a sudden flash of insight: it was thought out in a few hours—was written down with such a sketch of its various applications and developments as occurred to me at the moment,—then copied on thin letter-paper and sent off to Darwin—all within one week. *I* was then (as often since) the ' young man in a hurry '; *he*, the painstaking

and patient student, seeking ever the full demonstration of the truth he had discovered, rather than to achieve immediate personal fame.

"Such being the actual facts of the case, I should have had no cause for complaint if the respective shares of Darwin and myself in regard to the elucidation of nature's method of organic development, had been thenceforth estimated as being, roughly, proportional to the time we had each bestowed upon it when it was thus first given to the world—that is to say, as twenty years is to one week. For, he had already made it his own. If the persuasion of his friends had prevailed with him, and he had published his theory after ten years', fifteen years', or even eighteen years' elaboration of it, *I* should have had no part in it whatever, and *he* would have been at once recognized, and should be ever recognized, as the sole and undisputed discoverer and patient investigator of the great law of 'Natural Selection' in all its far-reaching consequences.

"It was really a singular piece of good luck that gave me any share whatever in the discovery . . . it was only Darwin's extreme desire to perfect his work that allowed me to come in, as a very bad second, in the truly Olympian race in which all philosophical biologists, from Buffon and Erasmus Darwin to Richard Owen and Robert Chambers were more or less actively engaged."

ECHOES OF THE STORM

It is impossible to do more than refer briefly to the storm of opposition with which the *Origin* was at first received. The reviewer in the *Athenæum* for November 19, 1859, left the author "to the mercies of the Divinity Hall, the College, the Lecture Room, and the Museum."[1] Dr. Whewell for some years refused to allow a

[1] *Life and Letters,* II, p. 228 n.

copy of the *Origin* to be placed in the library of Trinity College, Cambridge.[1] My predecessor, Professor J. O. Westwood, proposed to the last Oxford University Commission the permanent endowment of a Reader to combat the errors of Darwinism. "Lyell had difficulty in preventing [Sir William] Dawson reviewing the *Origin* on hearsay, without having looked at it. No spirit of fairness can be expected from so biased a judge."[2] And even when naturalists began to be shaken by the force of Darwin's reasoning, they were often afraid to own it. Thus Darwin wrote to H. Fawcett, on September 18, 1861:—

> "Many are so fearful of speaking out. A German naturalist came here the other day; and he tells me that there are many in Germany on our side, but that all seem fearful of speaking out, and waiting for some one to speak, and then many will follow. The naturalists seem as timid as young ladies should be, about their scientific reputation."[3]

Among the commonest criticisms in the early days, and one that Darwin felt acutely,[4] was the assertion that he had deserted the true method of scientific investigation. One of the best examples of this is to be found in the letter, December 24, 1859, of Darwin's old teacher in geology, Adam Sedgwick:—

[1] *Life and Letters*, II, p. 261.
[2] From a letter written by Darwin, November 4, 1862. *More Letters*, I, p. 468.
[3] *More Letters*, I, p. 196.
[4] See Darwin's letter to Henslow, May 8, 1860. *More Letters*, I, pp. 149, 150.

"You have *deserted*—after a start in that tram-road of all solid physical truth—the true method of induction, and started us in machinery as wild, I think, as Bishop Wilkins's locomotive that was to sail with us to the moon." [1]

These wild criticisms were soon set to rest by Henry Fawcett's article in *Macmillan's Magazine* in 1860 and by a paper read before the British Association by the same author in 1861. Referring to this defense, Fawcett wrote to Darwin, July 16, 1861:—

"I was particularly anxious to point out that the method of investigation was in every respect philosophically correct. I was spending an evening last week with our friend Mr. John Stuart Mill, and I am sure you will be pleased to hear that he considers your reasoning throughout is in the most exact accordance with the strict principles of logic. He also says the method on investigation you have followed is the only proper one to such a subject. It is easy for an antagonistic reviewer, when he finds it difficult to answer your arguments, to attempt to dispose of the whole matter by uttering some such commonplace as 'This is not a Baconian induction.'"

. . . .

"As far as I am personally concerned, I am sure I ought to be grateful to you, for since my accident nothing has given me so much pleasure as the perusal of your book. Such studies are now a great resource to me." [2]

[1] *Life and Letters*, II, p. 248. See also the *Quarterly Review* for July, 1860. Sedgwick's review in the *Spectator*, March 24, 1860, contains the following passage: " . . . I cannot conclude without expressing my detestation of the theory, because of its unflinching materialism; because it has deserted the inductive track, the only track that leads to physical truth; because it utterly repudiates final causes, and thereby indicates a demoralized understanding on the part of its advocates." Quoted in *Life and Letters*, II, p. 298.

[2] *More Letters*, I, pp. 189, 190.

To this Darwin replied:—

"You could not possibly have told me anything which would have given me more satisfaction than what you say about Mr. Mill's opinion. Until your review appeared I began to think that perhaps I did not understand at all how to reason scientifically." [1]

THE MATURITY OF THE *ORIGIN* CONTRASTED WITH THE CRUDITY OF RIVAL INTERPRETATIONS

It is remarkable to contrast the maturity, the balance, the judgment, with which Darwin put forward his views, with the rash and haphazard objections and rival suggestions advanced by his critics. It is doubtful whether so striking a contrast is to be found in the history of science;—on the one side twenty years of thought and investigation pursued by the greatest of naturalists, on the other offhand impressions upon a most complex problem hastily studied and usually very imperfectly understood. It is not to be wondered at that Darwin found the early criticisms so entirely worthless. The following extract from an interesting letter [2] to John Scott, written on December 3, 1862, shows how well aware he was of difficulties unnoticed by critics:—

"You speak of difficulties on Natural Selection: there are indeed plenty; if ever you have spare time (which is not likely, as I am sure you must be a hard worker) I should be very glad to hear difficulties from one who has observed so much as you have. The major-

[1] *More Letters,* I, p. 189.

[2] *More Letters,* II, p. 311.

ity of criticisms on the *Origin* are, in my opinion, not worth the paper they are printed on."

From the very first the most extraordinarily crude and ill-considered suggestions were put forward by those who were unable to recognize the value of the theory of Natural Selection. A good example is to be found in Andrew Murray's principle of a sexual selection based on contrast,—" the effort of nature to preserve the typical medium of the race." [1] And even in these later years the wildest imaginings may be put forward in all seriousness as the interpretation of the world of living organisms. Thus in Beccari's interesting work on Borneo,[2] the author compares the infancy and growth of the organic world with the development and education of an individual. In youth the individual learns easily, being unimpeded by the force of habits, while " with age heredity acts more strongly, instincts prevail, and adaptation to new conditions of existence and to new ideas becomes more difficult; in a word, it is much less easy to combat hereditary tendencies." Similarly in the state of maturity now reached by the organic world Beccari believes that the power of adaptation is well-nigh non-existent. Heredity, through long accumulation in the course of endless generations, has become so powerful that species are now stereotyped and cannot undergo advantageous changes.

[1] *Life and Letters*, II, p. 261.

[2] *Wanderings in the Great Forests of Borneo*, London, 1904. English translation, pp. 209-16.

For the same reason acquired characters cannot now be transmitted to offspring. Beccari imagines that everything was different in early ages when, as he supposes, life was young and heredity weak. In this assumed "Plasmatic Epoch" the environment acted strongly upon organisms, evoking the responsive changes which have now been rendered fixed and immovable by heredity.

Even the hypothesis proposed as a substitute for Natural Selection by so distinguished a botanist as Carl Nägeli turns out to be most unsatisfactory the moment it is examined. The idea of evolution under the compulsion of an internal force residing in the idioplasm is in essence but little removed from special creation. On the subject of Nägeli's criticisms Darwin wrote,[1] August 10, 1869, to Lord Farrer:—

> "It is to me delightful to see what appears a mere morphological character found to be of use. It pleases me the more as Carl Nägeli has lately been pitching into me on this head. Hooker, with whom I discussed the subject, maintained that uses would be found for lots more structures, and cheered me by throwing my own orchids into my teeth."

DARWIN'S GREATEST FRIENDS IN THE TIME OF STRESS

It is interesting to put side by side passages from two letters [2] written by Darwin to Hooker, one in 1845 at the beginning of their friendship,

[1] *More Letters,* II, p. 380.
[2] *L. c.,* I, p. 39. The passages here quoted are put side by side by the editors of this work.

the other thirty-six years later, a few months before Darwin's death. The first shows the instant growth of their friendship: "Farewell! What a good thing is community of tastes! I feel as if I had known you for fifty years. Adios."

The second letter expresses at the end of Darwin's life the same feelings which find utterance ever and again throughout the long years of his friendship.

> "Your letter has cheered me, and the world does not look a quarter so black this morning as it did when I wrote before. Your friendly words are worth their weight in gold."

The friendship with Asa Gray began with a meeting at Kew some years before the publication of Natural Selection. Darwin soon began to ask for help in the work, which was ultimately to appear as the *Origin*. The following letter to Hooker, June 10, 1855, shows what he thought of the great American botanist:—

> "I have written him a very long letter, telling him some of the points about which I should feel curious. But on my life it is sublimely ridiculous, my making suggestions to such a man." [1]

The friendship ripened very quickly, so that on July 20, 1856, Darwin gave Asa Gray an account of his views on evolution,[2] and on September 5 of the following year a tolerably full description [3]

[1] *More Letters*, I, p. 418. Asa Gray's generous reply is printed on p. 421.
[2] *Life and Letters*, II, p. 78.
[3] *L. c.*, pp. 119, 120.

of Natural Selection. From this latter letter Darwin chose the extracts which formed part of his section of the joint essay published July 1, 1858.

Asa Gray's opinion on first reading the *Origin* was expressed not to Darwin but to Hooker in a letter written January 5, 1860:—

> "It is done in a *masterly manner*. It might well have taken twenty years to produce it. It is crammed full of most interesting matter—thoroughly digested—well expressed—close, cogent, and taken as a system it makes out a better case than I had supposed possible. . . ."

After attending to Agassiz's unfavorable opinion of the book, he continues: "Tell Darwin all this. I will write to him when I get a chance. As I have promised, he and you shall have fair play here. . . ."[1] A little later, when on January 23, he wrote to Darwin himself, Asa Gray concluded: "I am free to say that I never learnt so much from one book as I have from yours."[2]

It is impossible to do justice on the present occasion to the numerous letters in which Darwin expressed his gratitude for the splendid manner in which Asa Gray kept his word and "fought like a hero in defense."[3] At a time when few naturalists were able to understand the drift of Darwin's argument, the acute and penetrating mind of Asa Gray had in a moment mastered every detail. Thus Darwin wrote on July 22,

[1] *Life and Letters,* II, p. 268.
[2] *L. c.*, p. 272.
[3] *L. c.*, p. 310.

1860, concerning the article in the *Proceedings* of the American Academy for April 10:—

"I can not resist expressing my sincere admiration of your most clear powers of reasoning. As Hooker lately said in a note to me, you are more than *any one* else the thorough master of the subject. I declare that you know my book as well as I do myself; and bring to the question new lines of illustration and argument in a manner which excites my astonishment and almost my envy! . . . Every single word seems weighed carefully, and tells like a 32-pound shot."[1]

Some weeks later, on September 26, 1860, Darwin again expressed the same admiration, and stated that Asa Gray understood him more perfectly than any other friend:—

" . . . You never touch the subject without making it clearer. I look at it as even more extraordinary that you never say a word or use an epithet which does not express fully my meaning. Now Lyell, Hooker, and others, who perfectly understand my book, yet sometimes use expressions to which I demur."[2]

Darwin also sent[3] Asa Gray's defense of the *Origin* to Sir Charles Lyell, whom he was extremely anxious to convince of the truth of evolution. Asa Gray's religious convictions prevented the full acceptance of Natural Selection. He was ever inclined to believe in the Providential guidance of the stream of variation. He also differed from Darwin in the interpretation of all instincts as congenital habits.[4]

[1] *Life and Letters*, II, p. 326. [2] *L. c.*, pp. 344, 345.
[3] *More Letters*, I, p. 169.
[4] *Life and Letters*, III, p. 170.

The same close intimacy and mutual help begun in the preparation of the *Origin* was continued in Darwin's later botanical works. Thus Darwin owed his *Climbing Plants* to the study of a paper by Asa Gray, and he dedicated his *Forms of Flowers* to the American botanist "as a small tribute of respect and affection." Concerning some of the researches which afterward appeared in this book, Darwin wrote:[1] "I care more for your and Hooker's opinion than that of all the rest of the world, and for Lyell's on geological points."

Another great name, that of Huxley, is especially associated in our minds with the defeat of those who would have denied that the subject was a proper one for scientific investigation. In the strenuous and memorable years that followed the appearance of the *Origin* the mighty warrior stands out as the man to whom more than to any other we owe the gift of free speech and free opinion in science,—the man so admirably described by Sir Ray Lankester at the Linnean celebration, "the great and beloved teacher, the unequaled orator, the brilliant essayist, the unconquerable champion and literary swordsman—Thomas Henry Huxley."

Comparing the friendships to which Darwin owed so much, Lyell was at first the teacher but finally the pupil,—unwilling and unconvinced at the outset, in the end convinced although still

[1] *Life and Letters*, III, p. 300.

unwilling; Hooker in England and Asa Gray in America were the two intimate friends on whom he chiefly depended for help in writing the *Origin* and for support to its arguments; Huxley was the great general in the field where religious convictions, expressed or unexpressed, were the foundation of a fierce and bitter antagonism.

THE ATTACKS OF RICHARD OWEN AND ST. GEORGE MIVART

An unnecessary bitterness was imported into the early controversies in England, because of the personality of the scientific leaders in the attacks on the *Origin*. Of these the chief was the great comparative anatomist, Richard Owen. In spite of his leading scientific position, this remarkable man withdrew from contact with his brother zoölogists, living in a self-imposed isolation which tended towards envy and bitterness. The same unavailing detachment had been carried much further by the great naturalist W. J. Burchell, who, as from a watch-tower, looked upon the world he strove to avoid with an absorbed and jealous interest. Professor J. M. Baldwin has shown how inevitable and inexorable is the grip of the social environment: the more we attempt to evade it the more firmly we seem to be held in its grasp.

In the first years of the struggle Owen's bitter antagonism made itself felt in the part he took as "crammer" to the Bishop of Oxford, and in

his anonymous article in the *Edinburgh Review* for April, 1860. But Owen could not bear to remain apart from the stream of thought when there was no doubt about the way it was flowing, so that in a few years he was maintaining some of the chief conclusions of the *Origin,* although retracting nothing, but rather keeping up his bitter attacks upon Darwin. This treatment received from one who was all affability [1] when they met was naturally resented by Darwin, whose feelings on the subject are expressed in the following passage from a letter to Asa Gray,[2] July 23, 1862:—

"By the way, one of my chief enemies (the sole one who has annoyed me), namely Owen, I hear has been lecturing on birds; and admits that all have descended from one, and advances as his own idea that the oceanic wingless birds have lost their wings by gradual disuse. He never alludes to me, or only with bitter sneers, and coupled with Buffon and the *Vestiges.*"

In the historical sketch added to the later editions of the *Origin,* Owen is the only writer who is severely dealt with. In this introductory section Darwin said that he was unable to decide whether Owen did or did not claim to have originated the theory of Natural Selection.[3]

About twelve years after the appearance of the *Origin* another opponent, St. George Mivart,

[1] "Mrs. Carlyle said that Owen's sweetness always reminded her of sugar of lead." *Life and Letters of T. H. Huxley,* London, II, p. 167.

[2] *More Letters,* I, p. 203.

[3] *Origin of Species,* 6th ed., p. xviii.

produced something of the same bitterness as Owen and for a similar reason. Thus Darwin wrote[1] to Hooker, September 16, 1871, as follows:—

> "You never read such strong letters Mivart wrote to me about respect towards me, begging that I would call on him, etc., etc.; yet in the *Q. Review* [July, 1871] he shows the greatest scorn and animosity towards me, and with uncommon cleverness says all that is most disagreeable. He makes me the most arrogant, odious beast that ever lived. I can not understand him; I suppose that accursed religious bigotry is at the root of it. Of course he is quite at liberty to scorn and hate me, but why take such trouble to express something more than friendship? It has mortified me a good deal."

On other occasions at a much later date I have myself observed that there was something peculiar about the poise of Mivart's mind, which seemed ever inclined to pass with abrupt transition from the extreme of an unnecessary effusiveness to an unnecessarily extreme antagonism.

Mivart's attack, contained in his book *The Genesis of Species,* was effectively dealt with by Chauncey Wright in the *North American Review* for July, 1871. Darwin was so pleased with this defense that he obtained the author's permission for an English reprint,[2] and with further additions it was published as a pamphlet by

[1] *More Letters,* I, p. 333. See also *Life and Letters,* III, p. 147.

[2] The pamphlet was published at Darwin's expense. For his keenly appreciative letter to the author see *Life and Letters,* III, p. 145.

John Murray in 1871. A copy presented by Darwin to the late J. Jenner Weir and now in the Library of the Hope Department of Oxford University Museum contains an interesting holograph letter referring to the pamphlet and bearing upon the controversy that followed upon the appearance of Mivart's book. This letter is, by kind permission of the Darwin family, now made public:—

"Down,
"Beckenham, Kent.
"Oct. 11, 1871.

"My dear Sir

"I am much obliged for your kind note & invitation. I sh^{d} like exceedingly to accept it, but it is impossible. I have been for some months worse than usual, & can withstand no exertion or excitement of any kind, & in consequence have not been able to see anyone or go anywhere.—As long as I remain quite quiet, I can do some work, & I am now preparing a new and cheap Edit^{n} of the Origin in which I shall answer Mr. Mivart's chief objections. Huxley will bring out a splendid review on d° in the *Contemporary R.*, on November 1st.

"I am pleased that you like Ch. Wright's article. It seemed to me very clever for a man who is not a naturalist. He is highly esteemed in the U. States as a Mathematician & sound reasoner.

"I wish I could join your party.—

"My dear Sir

"Yours very sincerely

"CH. DARWIN."[1]

Chauncey Wright speaks of presenting, in his review of Mivart, considerations "in defense and

[1] The letter is addressed to J. Jenner Weir, Esq., 6 Haddo Villas, Blackheath, London, S. E.

illustration of the theory of Natural Selection. My special purpose," he continues, "has been to contribute to the theory by placing it in its proper relations to philosophical inquiries in general."[1]

This able critic in America and Henry Fawcett in England represent a class of thinkers who have taken and still take a very important part in upholding the theory of Natural Selection. It is not necessary to be a biologist in order to comprehend the details and the bearings of this theory. They were at the very first understood by able thinkers who were not scientific men or who followed some non-biological science, when naturalists themselves were hopelessly puzzled. And at the present time such support is of the highest importance when within the limits of the sciences most nearly concerned the intense and natural desire to try all things is not always accompanied by the steadfast purpose to hold fast that which is good.

LAMARCK'S HYPOTHESIS AND THE HEREDITARY TRANSMISSION OF ACQUIRED CHARACTERS

The greatest change in evolutionary thought since the publication of the *Origin* was wrought, after Darwin's death, by the appearance of that wonderful and beautiful theory of heredity, which looks on parents as the elder brother and sister of their children. In this theory, itself an outcome of minute and exact observation,

[1] *Life and Letters,* III, pp. 143, 144.

Weismann raised the question of the hereditary transmission of acquired characters, the very foundation of Lamarckian evolution. Darwin accepted such transmission, and it was in order to account for "the inherited effects of use and disuse, &c.," [1] that he thought out his marvelous hypothesis of pangenesis. If such effects be not transmitted pangenesis becomes unnecessary and Weismann's simpler, more convincing, and better supported hypothesis of the continuity of the germ-plasm takes its place. It is impossible on the present occasion to speak in any detail of the controversy which has raged intermittently during the past twenty years on this fascinating subject. I will, however, briefly consider a single example of the error into which, as I believe, Darwin was led by following the Lamarckian theory of hereditary experience. I refer to the interpretation which he suggests for feelings of "the sublime," applying this term to the effect upon the brain of a vast cathedral, a tropical forest, or a view from a mountain height. Thus, writing to E. Gurney, July 8, 1876, Darwin said on this subject:—". . . possibly the sense of sublimity excited by a grand cathedral may have some connection with the vague feelings of terror and superstition in our savage ancestors, when they entered a great cavern or gloomy forest." [2]

An interesting account is given by Romanes [3]

[1] See the letter to Huxley, July 12 (1865?), in *Life and Letters,* III, p. 44.

[2] *Life and Letters,* III, p. 186.

[3] *Ibid.,* pp. 54, 55. See also I, pp. 64, 65.

of Darwin's own experience of these feelings, relating how he at first thought that they were most excited by the magnificent prospect surveyed from one of the summits of the Cordilleras, but afterwards came down from his bed on purpose to correct this impression, saying that he felt most of the sublime in the forests of Brazil.

We may first observe that the remarkable feelings induced by such experiences are very far from unpleasant, as we should expect them to be on the theory which refers them to the apprehensions and dangers of our primitive ancestors. Thus, on May 18, 1832, when the first impressions of a Brazilian forest were freshest in Darwin's mind, he wrote to Henslow, telling him of an expedition of 150 miles from Rio de Janeiro to the R. Macao.

> "Here I first saw a tropical forest in all its sublime grandeur—nothing but the reality can give any idea how wonderful, how magnificent the scene is. . . . I never experienced such intense delight. I formerly admired Humboldt, I now almost adore him; he alone gives any notion of the feelings which are raised in my mind on first entering the tropics."[1]

Furthermore, how are we to account on any such hypothesis for the similarity of the feelings excited by the forest, where enemies might lurk unseen, and the mountain peak, the very spot which offers the best facility for seeing them? It is also difficult to understand why the terrors of primitive man should be specially associated with

[1] *Life and Letters*, I, pp. 236, 237.

caves or with the most magnificent forests on the face of the earth. There is no valid reason for believing that any less danger lurked amid trees of ordinary size or lay in wait for him by the riverside, in the jungle, or the rock-strewn waste. In the midst of life he was in death in every solitary place that could afford cover to an enemy; on the mountain top probably least of all.

The feelings inspired by the interior of a cathedral are especially instructive in seeking the explanation of the psychological effect. We may be sure that the result is here produced by the unaccustomed scale of the esthetic impression. A cathedral the size of an ordinary church would not produce it. However intensely we may admire, the sense of the sublime is not excited or but feebly excited by the exterior of a cathedral, nor does it accompany the profound intellectual interest aroused by the sight of the pyramids. The thrill of the sublime, in the sense in which the term is here used, is, I do not doubt, the result of surprise and wonder raised to their highest power —a psychological shock at the reception of an esthetic visual experience on an unwonted scale, —vast as if belonging to a larger world in which the insignificance of man is forced upon him. It is not excited by the pyramids which are in form but symmetrical hills of stone, nor does the exterior of any building afford an experience sufficiently remote to produce the feeling in any high degree.

W. J. Burchell, in one of his letters[1] to Sir William Hooker, points out that the feelings of awe and wonder aroused in a Brazilian forest are not to be expected in those to whom the sight is familiar. As regards the depth and nature of the effects produced by the experiences here referred to, it would be very interesting to compare the savage with the civilized man, the uneducated with the educated mind. That the results are intimately bound up with the psychological differences between individuals—in part inherent, in part due to training and experience—is well illustrated in a story told by the late Charles Dudley Warner, who took two English friends to see for the first time the Grand Canyon of the Colorado. When they reached the point where the whole prospect—boundless beyond imagination—is revealed in a moment of time, one of his friends burst into tears, while the other relieved his feelings by unbridled blasphemy.

The remarkable psychological effects of a grandeur far transcending and far removed from ordinary experience may be compared to the thrill[2] so often felt on hearing majestic music, a thrill we do not seek to explain as a faint, far-off reminiscence of dread inspired by the savage war-cry. I do not doubt that an explanation of the sublime based on the terrors of our primitive an-

[1] Preserved in the Library at Kew, but, I believe, as yet unpublished.

[2] Darwin spoke of his backbone shivering during the anthem in King's College chapel. *Life and Letters*, I, p. 49; see also p. 170.

cestors is an example of the mistaken interpretations into which even Darwin was led by following the hypothesis of Lamarck.

FRANCIS DARWIN ON THE TRANSMISSION OF ACQUIRED CHARACTERS

One of the most recent attempts to defend the Lamarckian doctrine of the hereditary transmission of acquired characters is contained in the important Presidential Address of Mr. Francis Darwin to the British Association at Dublin (1908). In this interesting memoir the author expresses his belief that such transmission is implied by the persistence of the successive developmental stages through which the individual advances toward maturity. Following Hering and Richard Semon he is disposed to explain the hereditary transmission of these stages by a process analogous to memory. It is interesting to observe that this very analogy had been brought before Charles Darwin, but failed to satisfy him. He wrote [1] to G. J. Romanes, May 29, 1876:—

[1] *More Letters, I,* p. 364. See also the following sentence in a letter on Pangenesis, written June 3, 1868, to Fritz Müller: "It often appears to me almost certain that the characters of the parents are 'photographed' on the child, only by means of material atoms derived from each cell in both parents, and developed in the child." *More Letters,* II, p. 82. The following passage in a letter to Sir Joseph Hooker, February 28, 1868, is also of great interest: "When you or Huxley say that a single cell of a plant, or the stump of an amputated limb, has the 'potentiality' of reproducing the whole or 'diffuse an influence,' these words give me no positive idea;—but when it is said that the cells of a plant, or stump, include atoms derived from every other cell of the whole organism and capable of development, I gain a distinct idea." *Life and Letters,* III, p. 81.

"I send by this post an essay by Häckel attacking Pan. and substituting a molecular hypothesis. If I understand his views rightly, he would say that with a bird which strengthened its wings by use, the formative protoplasm of the strengthened parts became changed, and its molecular vibrations consequently changed, and that these vibrations are transmitted throughout the whole frame of the bird, and affect the sexual elements in such a manner that the wings of the offspring are developed in a like strengthened manner. . . . He lays much stress on inheritance being a form of unconscious memory, but how far this is a part of his molecular vibration, I do not understand. His views make nothing clearer to me; but this may be my fault."

Should it hereafter be proved that acquired characters are transmitted, I can not but think that the interpretation will be on the lines of Charles Darwin's hypothesis of Pangenesis. But the probability that any such result will be established, already shown to be extremely small, has become even more remote in the light of the recent investigations conducted by Mendelians and mutationists.

For the transmission of all inherent qualities, including the successive stages of individual development, Weismann's hypothesis of the continuity of the germ-plasm supplies a sufficient mechanism. I remember, more than twenty years ago, asking this distinguished discoverer how it was that the hypothesis arose in his mind. He replied that when he was working upon the germ-cells of Hydrozoa he realized that he was dealing with material which early and late in the history of the individual was most carefully

preserved as if of the most essential importance for the species. If the efficient cause of the stages of ontogeny resides in the fertilized ovum—as we cannot doubt—Weismann's hypothesis satisfactorily accounts for their hereditary transmission. For the portion of the ovum set aside to form the germ-cells from which the next generation will arise is reserved with all its powers and includes the potentiality of these stages no less than the other inherent characteristics of the individual.

It is, I think, unfortunate to seek for analogies—and vague analogies they must always be—between heredity and memory. However much we have still to learn about it, memory is, on its physiological side, a definite property of certain higher cerebral tissues,—a property which has clearly been of the utmost advantage in the struggle for life and bears the stamp of adaptation. Compare, for instance, the difficulty in remembering a name with the facility in recognizing a face. Adaptation would appear to be even more clearly displayed in the unconscious registration in memory and the instant recognition of another individual as seen from behind or when partially concealed. Such memory is quite independent of the artistic power. Without any intelligent appreciation of what is peculiar to another individual, his characteristic features are stored up unconsciously so that when seen again he is instantly recognized.

One other consideration brought forward by Mr. Francis Darwin may be briefly discussed. It is well known that plants have the power of adjusting themselves to their individual environment, and that such adjustment may beneficially take the place of a rigid specialization. The static condition of plants renders this power especially necessary for them, and the hereditary transmission of the results of its exercise especially dangerous. Where the seed falls, there must the plant grow. The parent was limited to one out of many possible environments; the offspring may grow in any of them, and for one that would hit off the precise conditions of the parent and would benefit by inheriting the parental response, numbers would have to live in different surroundings and might be injured by the hereditary bias.

Mr. Francis Darwin calls attention to the leaves of the beech, which in the interior shaded parts of the tree possess a structure different from that exhibited in the outer parts more freely exposed to light. The structure of the shaded leaves resembles that apparently stereotyped in trees permanently adapted to shade, and Mr. Francis Darwin is inclined to regard the fixed condition as a final result of the hereditary transmission of the same response through a large number of generations.

The development of shade foliage in the beech is, I presume, a manifestation of a power widely

spread among animals and probably among plants also, a power of producing a definite individual adaptation in response to a definite stimulus. To stereotype the result would be to convert a benefit to the individual into an injury to the species. The beech in a very shady place would presumably develop the maximum of the shade foliage. How disadvantageous would the hereditary bias be to its offspring that happened to grow in more exposed situations. But, it is argued, in plants subject to the fixed condition we do meet with the fixed structure, just as if repetition had at length produced an hereditary result. The answer to this argument seems to me to be complete. When conditions are uniform and no power of individual adaptation is required, Natural Selection, without attaining the power, would produce the fixed result in the usual way. If, however, a species already possessing the power, ultimately came to live permanently in one set of conditions and thus ceased to need it, the power itself, no longer sustained by selection, would sooner or later be lost.

DARWIN'S VIEWS ON EVOLUTION BY "MUTATION"

It is interesting to note that the term "Mutation" appears at one time to have suggested itself to Darwin [1] in order to express the evolution or

[1] This seems clear from the following passage in a letter written February 14, 1845, to Rev. L. Blomefield (Jenyns): "Thanks for your hint about terms of 'mutation,' etc.; I had

descent with modification of species, by no means implying change by large and sudden steps as in the usual modern acceptation of the term. Indeed, the words "mutable," "mutability," and their opposites have never been employed with the special significance now attached to "mutation." Every one believes in the mutability of species, but opinions differ as to whether they change by mutation.

It is a mistake to suppose that Darwin did not long and carefully consider large variations, or "mutations," as supplying the material for evolution. Writing to Asa Gray as early as August 11, 1860, he said [1] of great and sudden variaation:—

> "I have, of course, no objection to this, indeed it would be a great aid, but I did not allude to the subject, for, after much labor, I could find nothing which satisfied me of the probability of such occurrences. There seems to me in almost every case too much, too complex and too beautiful adaptation in every structure to believe in its sudden production."

In the twenty years between 1860 and 1880 we find that Darwin was continually brought back to this subject by his correspondents, and by reviews and criticisms of his work. Scattered over

some suspicions that it was not quite correct, and yet I do not yet see my way to arrive at any better terms. It will be years before I publish, so that I shall have plenty of time to think of better words. Development would perhaps do, only it applied to the changes of an individual during its growth." *More Letters*, I, p. 50.

[1] *Life and Letters*, II, pp. 333, 334.

this period we find numbers of letters in which he expressed his disbelief in an evolution founded on "sudden jumps" or "monstrosities," as well as on "large," "extreme," and "great and sudden variations." Out of many examples I select one more because of its peculiar interest. The Duke of Argyll had criticised Darwin's theory of Natural Selection as though it had been a theory of mutation, an interpretation repudiated by Darwin.

The Duke of Argyll in his address[1] to the Royal Society of Edinburgh, December 5, 1864, had said:—"Strictly speaking, therefore, Mr. Darwin's theory is not a theory of the Origin of Species at all, but only a theory on the causes which lead to the relative success and failure of such new forms as may be born into the world." In a letter to Lyell (January 22, 1865), Darwin wrote concerning this argument of the Duke's:—

> "I demur . . . to the Duke's expression of 'new births.' That may be a very good theory, but it is not mine, unless he calls a bird born with a beak 1-100th of an inch longer than usual 'a new birth'; but this is not the sense in which the term would usually be understood. The more I work the more I feel convinced it is by the accumulation of such extremely slight variations that new species arise."[2]

I desire again to state most emphatically that, during the whole course of his researches and reflections upon evolution, Darwin was thoroughly

[1] *Scotsman,* December 6, 1864.
[2] *Life and Letters,* III, p. 33.

aware of the widespread large variations upon which the mutationist relies. He had the material before him, he formed his judgment upon it, and on this memorable day it seems specially appropriate to show how extraordinarily sure his scientific instincts were wont to be. This will be made clear by a few examples of the solution which Darwin found for problems which at the time had either not been attempted at all or had been very differently interpreted.

Darwin's explanation of coral islands and atolls, at first generally accepted, was afterwards called in question. Finally, the conclusive test of a deep boring entirely confirmed the original theory. Perhaps the most remarkable case is that of the permanence of ocean basins and continental areas, a view which Darwin maintained single-handed in Europe, although supported by Dana in America, against Lyell, Forbes, Wallace, Hooker, and all others who had written on the subject. Darwin considered it mere waste of time to speculate about the origin of life; we might as well, he said, speculate about the origin of matter. Nothing hitherto discovered has shaken this opinion, which is expressed almost in Darwin's words in Professor Arrhenius' recent work.[1] In the fascinating subject of geographical distribution we now know that Darwin anticipated Edward Forbes in explaining the alpine arctic forms as relics of the glacial period,

[1] *Worlds in the Making.* English translation, London, p. 190.

while he interpreted the poverty of Greenland flora and the reappearance of north temperate species in the southern part of South America as results of the same cause. Almost as soon as the facts were before him in Wollaston's memoirs, Darwin had interpreted the number of wingless beetles in oceanic islands as due to the special dangers of flight. He anticipated H. W. Bates' hypothesis of mimicry, but drove it from his mind because he did not feel confident about the geographical coincidence of model and mimic. Long before the *Origin* appeared Darwin had thought over and rejected the idea that the same species could have more than a single origin or could arise independently in two different countries—a hypothesis very popular in later years, but, I believe, now entirely abandoned.

I should wish to advance one consideration before concluding this section of my address. Certain writers on mutation seem to hold the view that Natural Selection alone prevents large variations from often holding the field and leading to great and rapid changes of form. Such a view is not supported by the history of species which inhabit situations comparatively sheltered from the struggle, such as fresh water, caves, certain islands, or the depth of the ocean. Organisms in these places tend to preserve their ancestral structure more persistently than in the crowded areas where Natural Selection holds more potent sway.

EVOLUTION CONTINUOUS OR DISCONTINUOUS

Darwin fully recognized the limit to the results which can be achieved by the artificial selection in one direction of individual variations. Thus he wrote,[1] August 7, 1869, to Sir Joseph Hooker:—

> "I am not at all surprised that Hallett has found some varieties of wheat could not be improved in certain desirable qualities as quickly as at first. All experience shows this with animals; but it would, I think, be rash to assume, judging from actual experience, that a little more improvement could not be got in the course of a century, and theoretically very improbable that after a few thousands [of years'] rest there would not be a start in the same line of variation."

The conception of evolution hindered or for a time arrested for want of the appropriate variations is far from new. The hypothesis of organic selection was framed by Baldwin, Lloyd Morgan, and Osborn to meet this very difficulty, as expressed in the following paragraph quoted from the present writer's address to the American Association for the Advancement of Science at the Detroit meeting, October 15, 1897:—

> "The contention here urged is that natural selection works upon the highest organisms in such a way that they have become modifiable, and that this power of purely individual adaptability in fact acts as the nurse by whose help the species . . . can live through

[1] *More Letters,* I, p. 314.

times in which the needed inherent variations are not forthcoming." [1]

It has already been shown that Darwin entirely recognized the limits which the variations now called "fluctuating" may set to the progress achieved by artificial selection, and that he admitted the necessity of waiting for a fresh "start in the same line." In this respect he agreed with modern writers on mutation; but differed from them, as has been already abundantly shown, in the magnitude assigned to the variations forming the steps of the onward march of evolution. His observation and study of nature led him to the conviction that large variations, although abundant, were rarely selected, but that evolution proceeded gradually and by small steps,—that it was "continuous," not "discontinuous."

In his presidential address [2] to the British Association at Cape Town in 1905, Sir George Darwin brought forward the following argument from analogy against the "continuous transformation of species":—

"In the world of life the naturalist describes those forms which persist as species; similarly the physicist speaks of stable configurations or modes of motion of matter; and the politician speaks of States. The idea at the base of all these conceptions is that of stability, or the power of resisting disintegration. In other words, the degree of persistence of permanence of a species, of a configuration of matter, or of a State

[1] *Development and Evolution.* J. M. Baldwin, New York, 1902, p. 350.

[2] *Report British Association,* 1905, p. 8.

depends on the perfection of its adaptation to its surrounding conditions."

After maintaining that the stability of states rises and declines, culminating when it reaches zero in revolution or extinction, and that the physicist witnesses results analogous with those studied by the politician and the historian, the author continues:—

"These considerations lead me to express a doubt whether the biologists have been correct in looking for continuous transformation of species. Judging by analogy we should rather expect to find slight continuous changes occurring during a long period of time, followed by a somewhat sudden transformation into a new species, or by rapid extinction." [1]

I do not, of course, doubt that there is reality in the analogy between the evolution of states and of species, but it is not, I submit, close enough to justify the author's reasoning from one to the other. The communities of the social Hymenoptera present much closer analogies with political states, and yet even here it would be unjustifiable to infer that the evolution of insect societies has been discontinuous.

[1] The following footnote is appended to Sir George Darwin's address:—"If we may illustrate this graphically, I suggest that the process of transformation may be represented by long lines of gentle slope, followed by shorter lines of steeper slope. The alternative is a continuous uniform slope of change. If the former view is correct, it would explain why it should not be easy to detect specific change in actual operation. Some of my critics have erroneously thought that I advocate specific change *per saltum.*"

In reply to this note it may be pointed out that "*per saltum* evolution" or "discontinuous evolution" differs from "continuous evolution" only in the steepness of the slope of change.

The analogy seems to me far looser between the changes of configuration of matter witnessed by the physicist and the modification of a species as a result of the struggle with its organic environment. The essential characteristics by which the evolutionary history of the organic world diverges widely from that of the inorganic is very clearly stated in the following brief passage from a letter[1] written by Charles Darwin to Sir Joseph Hooker, on November 23, 1856, just three years before the publication of the *Origin:*—

"Again, the slight differences selected, by which a race or species is at last formed, stands, as I think can be shown (even with plants, and obviously with animals), in a far more important relation to its associates than to external conditions. Therefore, according to my principles, whether right or wrong, I can not agree with your proposition that time, and altered conditions, and altered associates, are 'convertible terms.' I look at the first and last as *far* more important, time being important only so far as giving scope to selection."

THE FIFTIETH ANNIVERSARY OF THE *ORIGIN OF SPECIES;*—A RETROSPECT

That the *Origin of Species,* which Darwin described as undoubtedly the chief work of his life,[2] should have been bitterly attacked and misrepresented in the early years of the last half century, is quite intelligible; but it is difficult to understand the position of a recent writer who maintains that the book exercised a malignant influ-

[1] *Life and Letters,* II, p. 87.
[2] *Life and Letters,* I, p. 86.

ence upon the interesting and important study of species and varieties by means of hybridism. As regards these researches its appearance, we are told, "was the signal for a general halt";[1] upon them Natural Selection "descended like a numbing spell";[2] and if we are still unsatisfied with his fertility in metaphor the author offers a further choice between the forty years in the wilderness,[3] and the leading into captivity.[4]

Francis Galton, in his address as a recipient of the Darwin-Wallace medal on July 1st last, recalled the effect of the Linnean Society Essay and the *Origin*. The dominant feeling, he said, was one of freedom. This liberty was offered to the student of hybridism as freely as to any other. No longer brought up against the blank wall of special creation, he could fearlessly follow his researches into all their bearings upon the evolution of species. And this had been clearly foreseen by Darwin when, in 1837, he opened his first note-book and set forth the grand program which the acceptance of evolution would unfold. He there said of his theory that "it would lead to study of . . . heredity," that "it would lead to closest examination of hybridity and generation." In the *Origin* itself the admirable researches of Kölreuter and Gärtner on these very subjects received the utmost attention and were

[1] *Report British Association*, 1904, p. 575.
[2] *L. c.*, p. 576.
[3] *Mendel's Principles of Heredity*, W. Bateson, 1902, p. 104.
[4] *L. c.*, p. 208.

brought before the world far more prominently than they have ever been either before or since. Furthermore, the only naturalist who can be described as a pupil of Darwin's was strongly advised by him to repeat some of Gärtner's experiments.[1] It is simply erroneous to explain the neglect of such researches as a consequence of the appearance of the *Origin* and the study of adaptation. So far from acting as a " numbing spell " upon any other inquiry, adaptation itself has been nearly as much neglected as hybridism, and for the same reason—the dominant influence upon biological teaching of the illustrious comparative anatomist Huxley, Darwin's great general in the battles that had to be fought, but not a naturalist, far less a student of living nature.

The momentous influence of the *Origin* upon the past half century, as well as that strange lack of the historic sense which alone could render possible the comparisons I have quoted, require for their appreciation the addition of yet another metaphor to the series we have been so freely offered.

The effect of the *Origin* upon the boundless domain of biological thought was as though the sun had at length dispelled the mists that had long enshrouded a vast primeval continent. It might then perhaps be natural for some primitive

[1] Darwin's letter of December 11, 1862, to John Scott, contains the following words: " If you have the means to repeat Gärtner's experiments on variations of *Verbascum* or on maize (see the *Origin*), such experiments would be preëminently important."

chief to complain of the strong new light that was flooding his neighbors' lands no less than his own, thinking in error not inexcusable at the dawning of the intelligence of mankind, that their loss must be his gain.

And now in my concluding words I have done with controversy.

Fifty years have passed away, and we may be led to forget their deepest lesson, may be tempted to think lightly of the follies and the narrowness, as they appear to us, of the times that are gone. This in itself would be a narrow view.

The distance from which we look back on the conflict is a help in the endeavor to realize its meaning. Huxley's Address on *The Coming of Age of the Origin* was a pæan of triumph. Tyndall, his friend, further removed from the struggle by the nature of his life-work, realized its pathos when he spoke in his Belfast Address of the pain of the illustrious American naturalist who was forced to recognize the success of the teachings he could not accept,—the naturalist who dictated in the last year of his life the unalterable conviction that these teachings were false.

I name no names, but I think of leaders of organic evolution in this continent and in Europe, —sons of great men to whom the new thoughts brought the deepest grief, men who struggled tenaciously and indomitably against them. And full many a household unknown to fame was the

scene of the same poignant contrast, was torn by the same dramatic conflict.

We have passed through one of the world's mighty bloodless revolutions; and now, standing on the further side, we survey the scene and are compelled to recognize pathos as the ruling feature.

The sublime teachings which so profoundly transformed mankind were given by Him who came not to bring peace on earth but a sword. And so it is in all the ages with every high creative thought which cuts deep into " the general heart of human kind." It must bring when it comes division and pain, setting the hearts of the fathers against the children and the children against the fathers.

The world upon which the thoughts of Darwin were launched was very different from the world to which were given the teachings of Galileo and the sublime discoveries of Newton. The immediate effect of the first, although leading to the bitter persecution of the great Italian, was restricted to the leaders of the Church; the influence of the second was confined to the students of science and mathematics, and was slow in penetrating even these. Nor did either of these high achievements of the human intellect seriously affect the religious convictions of mankind. It was far otherwise with the teachings of the *Origin of Species;* for in all the boundless realm of philosophy and science no thought has brought with

it so much of pain, or in the end has led to so full a measure of the joy which comes of intellectual effort and activity as that doctrine of Organic Evolution which will ever be associated, first and foremost, with the name of Charles Robert Darwin.

THE THEORY OF NATURAL SELECTION FROM THE STANDPOINT OF BOTANY

BY

JOHN M. COULTER

The indebtedness of Botany to Charles Darwin extends beyond his formulation of the theory of the origin of species by Natural Selection. His historical position in plant physiology and in plant ecology is one of first rank, which these phases of Botany have often gratefully acknowledged. As for the theory of Natural Selection, its relation to the development of modern plant morphology is still more fundamental. It is true that about ten years before the appearance of the *Origin of Species,* Hofmeister had given to modern plant morphology its first great impulse in his demonstration of the essential relationships among higher plants; but the announcement of the theory of Natural Selection suggested a *modus operandi* for the plant phylogeny that may be said to have been established. Among plants, the facts and an outline of phylogeny for the application of any theory of descent had been secured, so that Natural Selection came to plant morphology at the psychological moment. It is no wonder that it was received by plant mor-

phologists with eagerness, and that it stimulated tremendously the type of investigation initiated chiefly by Hofmeister. Whether Natural Selection stands or falls as an adequate explanation of the origin of species, there can never be any doubt as to the breath of life it infused into the young science of phylogenetic plant morphology.

I am in no position to state whether from the standpoint of Botany the theory of Natural Selection presents any more difficulties or probabilities than it does from the standpoint of Zoölogy. The literature of the theory in its application to animals is so vast, and has become so special, that no botanist can be expected to compass it intelligently. The present series of papers may make this situation clear; and yet I cannot presume to speak for botanists in general, among whom there is great diversity of opinion. I can only express the opinion of an individual botanist who has had some experience in dealing with the facts that enter into the construction of phylogenies.

SELECTION DOES NOT ORIGINATE CHARACTERS

When the botanist confines his attention to a wide-ranging genus of numerous species, as the genus *Aster* in North America, for example, the origin of these species by Natural Selection would seem to be an adequate explanation of the situation. The variations are endless and in

every direction, the intergrades are innumerable, the habitats are exceedingly diverse, and Natural Selection would seem to necessitate just the result observed. In fact, the greatest American student of the genus, after a prolonged effort to detect and define the boundaries of its species, gave it as his private opinion that "there are no species in Aster." Of course this must be understood as an expression of despair rather than of belief, but it emphasizes the situation. With the wide-ranging genera showing this condition, it was not difficult to imagine that the sharp differences among isolated species are to be explained by the breaking up of their continuity; and so all species were swept into the category of Natural Selection.

On the other hand, when the botanist came to enlarge the horizon of his observation, and included the whole phylogeny of some great group of plants, or even the phylogeny of the whole plant kingdom, he began to have doubts as to the adequacy of Natural Selection as an explanation of all the changes. He has learned to regard this selection as a factor that perpetuates and perhaps develops certain characters, and that eliminates others; but he cannot discover how it can really originate new characters. The genus Aster, for example, is defined by a definite group of characters; and the species may be regarded as the selected variants of these same characters. The pattern changes, as in the kaleidoscope, but noth-

ing new has entered into any combination. But when the Aster boundary is crossed, and still more when the boundaries of Compositæ and then of Angiosperms are crossed, absolutely new characters are met on every hand; and still the phylogenetic connections seem convincing. For example, perhaps no plant morphologist doubts in these days that at least some of the Gymnosperms are phylogenetically related to ancient ferns. The distinguishing mark between the two groups is the absence of seeds in the one and their presence in the other. The seed and all that goes with it is a new character, and how selection could have originated it, is a question at whose answer even scientific imagination balks. It is evident that the ovules of Gymnosperms are related by descent to the sporangia of ferns in some way, but so extensive a change does not seem to come within the possibilities of Natural Selection. We have relatively primitive ovules, but they are enormously different from fern sporangia; and we can imagine how selection may have transformed these ovules into those of more advanced type, for this is only manipulating a structure already in existence and is adding nothing new. The leaves of sporophytes, the vascular system, the root system are further illustrations of the same kind. Absolutely unrepresented in the lower groups, they are new, complex, and fully functioning structures when we meet them first. Of course lost records and an inconceivable lapse

of time are the usual answers, but they do not save us from doubt.

In brief, by the botanist who has brought together a wide range of material, natural selection might be accepted as having variously arranged a group of established characters, and in this sense given rise to what we call species; but it could not be accepted so easily as originating such new characters as distinguish great groups. In a certain sense, of course, there is nothing new, or else there would be no phylogeny; but as we *use* the word *character,* it often appears as a new thing in passing from one great group to another one presumably derived from it.

NON-ADAPTIVE "ADAPTATIONS"

To the botanist, the greatest immediate difficulty with Natural Selection has probably come from the idea of adaptations associated with it. For a time he was captivated with the idea, and much botanical literature testifies to the fact. As he then understood it, nature selected those forms that are best adapted to their environment, and destroyed those that are less adapted. This meant that the characters of the forms selected for survival must show some fitness for the environment, and great ingenuity was displayed in explaining this fitness. Then came the new subject ecology and its associate experimental morphology, and the old explanations began to vanish.

For example, the character of thorns was said to be selected because their presence was a protection against grazing animals. Now it is known that thorns chiefly prevail among plants in regions peculiarly free from grazing animals; and that even if the grazing animals are present the thorns do not appear in the early stages of the plant, when they are most needed. Conversely, the plants chiefly attacked by grazing animals are singularly free from thorns. Experimental work has shown that many thorns are a response to poor nutrition, and that they may or may not become an established character.

The elaborate stinging hairs of the nettle represent a character that according to this view was built up by Natural Selection, with adaptation as the principle of selection. Now it is known that the nettle is indifferent to their presence and gets along without them.

It is a well-known fact that many seeds, especially those of arid regions, develop a testa so hard that it interferes with the breaking through of the embryo. In fact, it is becoming evident that if selection is working in these cases it is working towards "over-adaptation."[1]

A difficulty is also presented by such structures as the velamen of the aërial orchids, as well as by the water-conducting vessels of the vascular system. In both of these cases the structures do

[1] This situation has been developed by the recent studies of the germination of seeds and spores by Dr. William Crocker of the University of Chicago.

not perform their very important functions until the cells are dead. Just how a group of dead cells, performing a mechanical function, could have been built up by Natural Selection, is hard to imagine; and yet, in the case of the vascular system its presence is a fundamental distinction between two great divisions of the plant kingdom.

A striking illustration of the change of view that plant structures are necessarily useful because they have been selected on account of adaptation has been developed by a very recent investigation of extra-floral nectaries,[1] which included an examination of 100 species of plants growing in the Botanic Gardens of Buitenzorg, Java. The view in reference to many of these extra-floral nectaries has been that they attract ants, which in turn defend the host plant from its enemies. Hence we have such a category of plants as myrmecophiles, or "ant-loving plants." Darwin himself naturally believed in myrmecophiles, and Kerner included them among his illustrations of protection against "unbidden guests." Now it appears that any such use for these remarkable organs is untenable; and there are many facts that suggest that they have no definite purpose that could be laid hold of as an adaptation. The secretion often begins late in the life of the plant, so that any protection it affords is lacking

[1] Nieuwenhuis von Uxküll-Güldenbandt, M.: "Extraflorale Zuckerausscheidungen und Ameisenschutz," *Ann. Jard. Bot. Buitenzorg*, II, 6; pp. 195-327. 1907.

when most needed. In some cases the secretion begins at a very early stage of the plant and soon fails, leaving the maturing and adult plants unprotected. The nectaries secrete spasmodically and are often dry; and the nectar of many forms is avoided by ants and other animals. There is no relation between mutilated flowers, ants, and extra-floral nectaries. Most mutilated flowers produce as many seeds as those that are not; and the honey-seeking ants are not combative and do not attack other insects visiting their host. If these extra-floral nectaries have been developed and perpetuated by Natural Selection, it is an illustration of the selection of harmful structures, for they often attract insects of all kinds, which damage the plant in various ways. The investigation showed that individual plants which secrete little or no nectar are less harmed by insects than are those that produce nectar.

It is such work that is playing havoc with the "adaptations" of botanical literature, and is forcing botanists to see in these various structures inevitable responses to conditions that have nothing to do with adaptation. It would be going too far to say that such results destroy absolutely all faith in the selection and development and fixing of adapted structures, but they do tend to weaken faith and to demand that every claimed case shall be subject to rigid experimental investigation. That there must be selection no one pretends to deny, so far as I know, but when the

selection includes unfavorable as well as favorable characters, it seems to have lost its motive.

And still, behind all this uncertainty as to the selection and perpetuation of small variations, as to whether this kind of indiscriminate selection can result in anything so definite as distinct species, there is clearly evident the large fact of the evolution of the plant kingdom, which has become a more difficult problem than ever before. To observe and explain the small results, which are the only kind that can be brought under the absolute control of modern investigation, seems to result in obtaining a measuring rod too short to apply to general phylogeny; and the more confusing are our experimental results, the larger becomes the error that is multiplied by the general application.

So far as I am acquainted with the opinions of botanists whose work has to do with structures and phenomena involved in evolution, there seems to be a general feeling that Natural Selection does not select individual plants on the basis of some small and better adapted variation, and so build up a character, which with its associates will gradually result in a closely allied new species; but that its selection of individuals seems to hold no relation to their useful characters. On the other hand, there is general conviction that Natural Selection determines what species shall survive, simply by eliminating those that do not. Applying this to a general phylogeny, Natural

Selection becomes a factor of enormous importance; for the species that survive determine, within limits, the species to be produced.

NON-UTILITY IN THE EVOLUTION OF GYMNOSPERMS

A general illustration of this point of view may be taken from the phylogenetic relationships among Gymnosperms. This ancient group stands among plants as one of remarkable rigidity. Land plants should be more plastic than land animals, for they must remain fixed in a given environment, while animals can shift their environment when the pressure of change comes. A striking contrast between the taxonomic characters used by zoölogists and those used by botanists is brought out here. Among botanists, the taxonomic characters in most general use are those that respond with least promptness or not at all to changing environment; while among zoölogists, as I am informed, the taxonomic characters in most general use largely fall in the category of so-called "adaptation" characters, which had far better be called "response" characters. For this very reason, I can easily imagine that there should be more supporters of Natural Selection among zoölogists than among botanists.

Be this as it may, Gymnosperms seem to be about the least plastic of land plants, certainly the least plastic of any great group. Even the

number of chromosomes, which in some groups of plants may vary from species to species, seems to be practically a fixed number in the whole assemblage. There seems to be among them little or no visible response in nature to changing conditions of the most extreme kinds. It would seem that selection among these relatively invariable forms can hardly be more than the accident of crowding. Certainly one can lay hold of no kind of variation in nature that even suggests the coming characters of another species, much less of another genus or family. And yet the group as a whole shows that certain distinct evolutionary tendencies have been worked out in a progressive way. Students of the group may differ as to the details of the phylogenetic history, but there is no difference of opinion as to its general features. Some of these general features may be instructive in this connection.

The plant which produces the female sex organs, known as the female gametophyte, is not only in the midst of an ovule invested by a thick integument, but is also directly inclosed by the heavy wall of the megaspore that produced it. If any structure is shut away from the influences of a changing environment, it would seem to be this one. And yet, through the whole series of Gymnosperms, this gametophyte shows a progressive transformation. In the most primitive forms it matures as a relatively large mass of tissue, and late in its history the female sex organs

(archegonia) appear. In the first stage of its development it consists of a large number of free nuclei; in the second stage walls appear and a tissue is formed; and in the last stage this tissue grows and finally produces the archegonia with their egg. The constant tendency throughout the whole group is to produce the female sex organs earlier and earlier in the history of the gametophyte. A series can be arranged illustrating the appearance of the sex organs at what might be called the mature stage of the gametophyte, at one extreme; then their appearance at earlier and earlier stages of the tissue development, until they appear with the first formation of walls; and finally, at the other extreme, the eggs appear at the stage of free nuclei, so that no sex organs are formed. This progressive slipping back of the egg in the ontogeny of the gametophyte holds no relation to any advantage that can be detected. Certainly it holds no relation to any advantage in fertilization, for that is a prolonged process among Gymnosperms, and the pollen tube containing the sperms may live for a season or two in the tissues of the ovule. Taking the group as a whole, this is not a sporadic change, occurring here and there; but the two extremes I have given are the two extremes of the Gymnosperm phylum. This kind of progressive change is beyond the reach of experiment, and its explanation is beyond the reach of imagination as yet.

The same kind of progressive change is shown also in the embryo of Gymnosperms. In the most primitive condition, the first stage of embryo formation is extensive free nuclear division within the fertilized egg; after this, walls are formed and the egg becomes filled with tissue, the proembryo. Throughout the Gymnosperm series there is a steady reduction of the amount of free nuclear division, and with it a reduction of the amount of proembryonic tissue, so that finally it occupies a very small portion of the fertilized egg. All this change has taken place further from outside influences than the change in the gametophyte, for the embryo is imbedded in the gametophyte.

It may be claimed that these are not the characters that taxonomists use in distinguishing species. This is true, but they are just the characters that distinguish great groups, and represent the advancement of the plant kingdom as a whole. It so happens that both of the progressive changes noted as occurring among Gymnosperms culminate among Angiosperms.

The male gametophyte of Gymnosperms shows a similar progressive change, not so steady, but none the less evident. Its few cells are contained within the resistant wall of the pollen grain which produces it. In the more primitive condition the vegetative cells are variable in number, but evident; but there is a persistent tendency to eliminate them, which reaches comple-

tion in certain Gymnosperms, and is a constant feature of Angiosperms.

It may be said that in all these cases we are dealing with structures that have ceased to be useful, and therefore are being gradually eliminated. No one can say how useful they are, but no one can deny that they are functional. But there is a striking illustration of another sort among Gymnosperms. The suspensor is a conspicuous organ of the embryo in this group, with a development apparently out of all proportion to its usefulness. In fact, it is a most exaggerated structure, often becoming closely coiled on account of its extreme length. One would suppose that this would be the first structure eliminated, or at least curtailed, if usefulness determines suppression. But the suspensor of Gymnosperms shows no symptom of suppression throughout the whole group, and still among the heterosporous Pteridophytes below and the Angiosperms above, where the same conditions prevail, it shows no such unusual development.

Several illustrations could be taken from Gymnosperms, all of them fundamental in the structure and progress of the group, and none of them in use by taxonomists. My claim is that it may be one thing to pass from species to species within the limits of a small natural group; and a very different thing to pass from one great group to another. I do not doubt that the characters of a genus may have been juggled in a variety of

ways to form what we call its species, and that one of these ways may have been Natural Selection, with or without adaptation. Our problem, however, includes more than the origin of species. All of our observation and experimental work in this field is immensely important in demonstrating the theory of descent, and in showing how the final diversity of species is reached; but the methods for securing this final diversity may not apply and probably do not apply to the establishment of the assemblages of different characters that distinguish the great groups, and that any study of phylogeny shows to have been wrought out by steady and progressive change through all imaginable changes of environment. Species have been likened to the individual waves that appear on the surface of a choppy sea; if so, the deep-seated changes to which I refer, and which phylogeny makes so evident, may be likened to the great oceanic currents, whose movement and direction proceed with no relation to the choppy surface.

ISOLATION AS A FACTOR IN ORGANIC EVOLUTION

BY

DAVID STARR JORDAN

By isolation, segregation or separation as a factor in evolution, we mean the failure of a portion of one group or species to interbreed freely with the rest of its kind. Such failure is due to the presence of some barrier which prevents free intermingling of individuals or to some condition or group of conditions which sets certain individuals off from the mass of their kind. Through separations of this sort race distinctions arise, and in time by the same means the more profound modifications which mark what we call species. The occasion of divergence in most cases is found in geographical separation, the "raümliche Sonderung," on which such strong emphasis has been justly laid by Moritz Wagner. It may again be a separation of some other kind, as segregation, through the occupation of different tracts within the same general area, or seasonal separation, as when flowers bloom or animals mate at different times of the year. There are also forms of physiological segregation. Self-fertilized plants mate with their neighbors irregularly or by chance, the pure species standing alongside of

hybrids or quasi-hybrids. Dr. Shull informs us that several such cases occur in the flora of California. A race or species of higher animals may develop dislikes or infertilities with forms otherwise nearly related. Caton tells us that this is true of deer, which will not cross with other species unless "demoralized," or relieved of race antipathy, by enforced association.

LAW OF GEOGRAPHICAL DISTRIBUTION

Free interbreeding tends to unify or obliterate forms which are fertile with each other. Isolation in any form tends to check this process, and hence in negative fashion works to create new forms based on distinctions arising through natural variation and retained through heredity. From this fact arises the rule that closely related forms or nascent species do not as a rule inhabit or rather breed in the same area. This proposition has been termed by Dr. J. A. Allen "Jordan's Law of Geographical Distribution."

The law or generalization has been stated as follows:—

> "Given any species (or kind) in any region, the nearest related species (or kind) is not to be found in the same region, nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort, or at least by a belt of country, the breadth of which gives the effect of a barrier."

This law holds good as a general rule among animals. The only exceptions yet indicated are

found among plants in which cross-fertilization is not general, among Protozoa and other low forms in which specific distinctions are unknown or at least obscurely shown, in cases of isolation other than geographical, and in a few cases which seem to be explainable on the ground of re-invasion. It is possible that species once thoroughly separated through some form of geographical segregation may later invade the territory, the one of the other, without crossing or hybridization. This seems likely to occur among plants, and it is possible among migratory animals also. Taking the world over, re-invasion is probably not a rare phenomenon, although in most cases the invading species may fail to establish itself. In the case of animals dependent on man, we find sometimes a form of political segregation, which may lead to the separation of races without actual physical barriers. The races of sheep in England, for example, go by counties. The artificial boundary of a county is a barrier to man, rather than to the sheep. In all forms of artificial selection, a corresponding degree of artificial segregation is always implied and, without segregation, selection has no effectiveness in race-forming. Nothing, for example, can be done for the race improvement of fishes, unless these can be segregated in artificial ponds, away from the unselected mass of the species.

THE WAY ISOLATION WORKS

Isolation, as a factor in evolution, represents the failure of a species to unify itself or to maintain a homogeneous character among its members. Within a unified species, each member will be fertile with any other of the opposite sex. In time, the descendants of any one may cross with descendants of all the others, thus bringing all individuals to that degree of common relationship implied by membership in a common species. Wherever inter-crossing is checked along any line, a part of the individuals will be set off from the mass, and here divergence at once begins. One cause of divergence may lie in the fact that in each isolated group there is some original deviation from the average of the common stock, thus giving at the start some slight difference in heredity. But this is purely hypothetical and it is not probable in any special case. Other and apparently more potent causes of divergence lie in the difference of experiences to which each group is exposed. The stress of the struggle for existence is never quite the same in different localities, and the nature of selection must vary accordingly.

That notable differences obtain in time, even in pure stocks, and when there is no visible reason for change, is clearly shown in the experience of stock breeders. Of this, a typical example will suffice. Darwin tells us that the two flocks of

Leicester sheep, those of Mr. Buckley and of Mr. Burgess, were "purely bred from the original stock of Mr. Bakewell for fifty years." There is not a suspicion of a single instance of deviation from the pure Bakewell Leicester breed in either flock. Yet after fifty years the difference in the flocks of sheep is so great that they "have the appearance of being quite different varieties." In nature, as in domestication, individuals of the same race, animals or plants, prevented from inter-crossing for a long time, present at least the appearance of distinct varieties or species. A study of the weeds of the world, as they have spread from place to place, should show this fact in interesting fashion. It can also be shown by a comparative study of dogs or horses. Mr. Vernon Bailey tells me that in the pouched gophers and other rodent groups each valley has its individual peculiarities, those shown in the skulls as well as in the forms or colors of the animals. All these variations, too small to justify the use of technical names, form the beginnings of difference in subspecies. With more perfect isolation these characters would soon assume greater importance. They seem to indicate the beginning of species-forming.

So far as species in nature are concerned, we can account for the origin of none of them, except on the ground of the presence of some forms of isolation. In those groups of animals or plants which have been most studied, subspecies or vari-

eties are recognized only as a geographical limitation can be shown.

The known facts fully justify the statement by Dr. A. E. Ortmann that:—

> "The four factors named, variation, inheritance, selection, and separation, must work together to form different species. It is impossible to think that one of these should work by itself, or that one could be left aside."

To use a convenient analogy, the movement of organic evolution may be compared to the course of a stream. Isolation is the rocky ledge which *does* nothing, but whose resistance must determine the direction of the river's flow. Selection is the force that drives the stream along, and variation and heredity lie inherent in the nature of the stream of life itself. All of these are necessary in bringing about the final result, whatever that may be. With these there are doubtless other facts, extrinsic and intrinsic, but in this world of varied contour and of prodigal reproduction, no organism, whatever its heredity or its variations, can escape these limiting environmental conditions. Whatever takes part in the final result must be a factor in evolution, whether it be an initial factor in variation or not.

In the belief of the writer, the minor differences which separate species and subspecies among animals and plants, in so far as these are not traits of adaptation (and most of them are clearly not such), owe their existence to some

form of isolation or segregation. By the effect of some form of barrier the members of one group are prevented from interbreeding with those of another minor group or with the mass of the species. As a result, from difference of parentage, or difference in selection, or from difference in the trend of development, whatever its cause, local peculiarities arise. "Migration," says Dr. Coues (and by this he means the shifting of habitation), "holds species true; localization lets them slip"; or, rather, localization leaves them in differing conditions in the general process of averaging up the mass of the species. The peculiarities of the parents in an isolated group become intensified by in-breeding. These peculiarities become modified in some continuous direction by the selection induced by the characteristics of the local environment. They may possibly be changed, as some have imagined, in one way or another, by germinal reactions induced by impact of environment. It may be that change of environment sometimes excites germinal variation. In any event, a new form is sooner or later inevitable if the segregation is complete. This new form is never coincident in range with the parent species, nor with any other closely cognate or germinate form. Neither is it likely to be found in some remote part of the earth. The details of its distribution will be determined by the nature of the organism and by its relation to its environment. The struggle for existence is a

very different matter in different parts of the world of life. The competition with like forms, the struggle with unlike forms, the compromise with hard conditions of life, all these change at every angle, and the character of Natural Selection changes with them. The individual animals are mobile, as plants are not. They shift about and occupy their range more perfectly, while in plants their pollen and their seed have great advantages over animals. With a plant everything depends on where its seed is dropped. *Where* an animal is born or hatched is a matter of relative indifference. With plants, some seed is sure to reach almost every available point within the range of the species, while the vast majority of seeds never have a chance to germinate. All these, and every other point of difference, between one group of organisms and another, affect the nature and relative value of the different factors in divergence. They tend also to obscure the laws of distribution. But no law is invalidated by the occurrence of exceptions which come under some other rule or law.

The obvious immediate factor in the splitting apart of races or species is, therefore, in all groups, that of isolation. Behind this lies the primal factor of variation, continuous or discontinuous. Fluctuation, saltation or mutation, all these are one for the purposes of our present discussion. With these come the factor of heredity and the factor of selection, to which we must

ascribe all adaptive changes and apparently no others. Selection alone does not produce new species, although it may continuously modify old ones. Usually related species become modified in parallel fashion by selection. Through adaptations to special surroundings, selection may produce convergence of characters, often of such a character as to give a semblance of real homology. The selection of the desert gives the horned toad resemblance to the cactus; this deceives no one. But it may give one cactus a deceptive resemblance to another which is forced to adapt itself to exactly the same conditions.

It is not often that one species is distinguished from another by adaptive characters, or by any conceivable difference in fitness to the same conditions in life. In this regard all are fit, and the process of natural selection holds each one close to its possible limit so long as conditions remain constant.

SOME ILLUSTRATIONS OF THE RESULTS OF ISOLATION

The formation of different breeds of sheep through isolation and unconscious selection in the different counties of England, as elsewhere described by the writer, is apparently exactly parallel with the formation of species in nature. The formation and fixing of new breeds or races through conscious selection is exactly parallel with this, except that in conscious artificial selec-

tion the destruction of the less fit is more drastic than in nature and the segregation of the garden or the flock is more perfect than is ever found in field or forest. There are no natural barriers so effective as those which may be reared in field or garden.

The existence of cognate or "geminate species," as I have elsewhere called them, the one representing the other on opposite sides of some barrier, has been long recognized by naturalists. In a general way such species agree with each other in all the respects which usually distinguish species within the genus. Their differences appear in minor regards, characters of degree, or proportion; traits which we may safely suppose to be of more recent origin than the ordinary characters marking off species within the group.

Illustrations of geminate species of birds, mammals, fishes, reptiles, snails, crustaceans, insects, trees, flowers, are well known to students of these groups.

To take familiar examples, each well separated island in the West Indies has its own form of golden warbler. Each island in the East Indies has its own forms of reptiles, monkeys, snails, and fresh water fishes. Each island in Hawaii has its own species of each genus of Drepanine birds; each forest its own type of land snails. Each of the three groups of rookeries in Bering Sea has its own species of fur seal. Each section of the Isthmus of Panama has its geminate species of

fishes, representing nearly every genus or subgenus of the shore-water of Mexico. Each floral region of the northern hemisphere has its characteristic form of most of the widespread genera of trees or shrubs. Wherever a distinct barrier exists, geminate species may be found on the two sides of it, unless for one reason or another one of these forms has failed to maintain itself in the struggle for existence. If the barrier is imperfect, the two species are likely to intermingle, giving an intergradation of forms. The absence of such connecting series is the only distinction between a species and a subspecies or geographical variety which many naturalists recognize. A subspecies that lives permanently in the same region coincident in range with the species from which it springs is unknown in zoölogy.

DARWIN'S VIEW OF THE RÔLE OF ISOLATION

Assuming that this view of the relation of geographical distribution to species-forming is a correct one, it is interesting to note the attitude of Darwin in regard to it.

It is clear that Darwin had the basal conception of the views here set forth. His own work in South America and that of Wallace in the East Indies yielded similar conclusions, although with Darwin geographical studies were subordinated to other forms of evidence of the transformation of species. Isolation Darwin considered

mainly in its static aspects, not as a necessary or at least not a separate factor in evolution. "Each species," he says, "has been produced within one area and has migrated as far as it could." This statement may be taken as the central fact of our knowledge of geographical distribution. The distribution of each species covers the earth except in so far as it is unable to reach distant parts through barriers, or as it has been unable to maintain itself in regions which it has reached—or as it has, through selection and isolation, been changed in some part of its range into a different species. In this case as elsewhere selection and segregation must work together, the one producing adaptive divergence or adaptive convergence, the other non-adaptive divergence alone.

Darwin quotes from Wallace that "every species has come into existence coincident in space and in time with a pre-existing closely allied species." This coincidence is attributed, by Darwin and Wallace, to "descent with modification." The language quoted is perhaps obscure, but the meaning of Wallace is clearly a recognition of the mutual relations of geminate species.

Darwin further states: "I do not doubt that isolation is of considerable importance in the formation of new species." He goes on to say that: "On the whole I am inclined to believe that largeness of area is of more importance, especially in the production of species which will prove capa-

ble of enduring for a long period and of spreading widely." But he regards past isolation as a factor in this case also, for he says:—

> "Moreover, great areas, though now continuous owing to oscillations of level, will often have recently existed in a broken condition so that the good effects of isolation will generally to a certain extent have concurred.
>
> "In isolation in a small area, conditions will tend to be uniform, so that natural selection will tend to modify all the varying species throughout the area in the same manner in reference to the same conditions."

He goes on to show that in isolation, intercrossing with outside individuals will be prevented; that individuals will be freed from outside competition, a condition favorable or "giving time" for "improvement," that is, for adaptive divergence.

It will be noticed that Darwin uses the word "isolation" in its literal meaning of island-residence, and that he does not extend it to include segregation or separation by barriers. Yet a mountain lake or a river basin may be just as much isolated in a biological sense for its water animals as an island is for its land inhabitants. Darwin makes no effort to separate two sets of facts. The one is that a great continent or a great sea or a great river will contain at any point more species than a small continent, a small sea, or a small river basin. This is because the large area offers freer access for many different types of organisms. Its less perfect barriers

favor reinvasion, and each group will have some representatives in all available locations. The other fact is that the forms in the small area tend to be more sharply defined. They are better species, from the point of view of taxonomy, and the causes of their existence can be better traced. In our current studies of evolution, we are of necessity more analytical than Darwin. We would view as separate factors elements which to him were simply phases of Natural Selection. In artificial selection, segregation or isolation was taken by Darwin for granted. Natural Selection was to Darwin the same cause or factor related to natural processes. In his chapter on Geographical Distribution, Darwin shows an essentially modern grasp of the subject, though without analysis of the reasons why variations in distribution naturally persist.

Darwin says:—

> "The preservation of favorable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would be unaffected by natural selection, and would be left a fluctuating element."

It is clear that the completed process of Natural Selection as here indicated implies segregation also, especially if we are to explain how those forms bearing "fluctuating elements" are to be coördinated as species. It is, moreover, certain that in most groups, probably in all, the characters that distinguish species are these elements,

neither useful nor injurious. Unless we use "Natural Selection" to cover both processes, as Darwin certainly would have done, we must assign to selection the preservation and intensification of adaptive characters, and to segregation the seizing and fixing of the non-useful, usually fluctuating, element. It is, however, a fact well known to breeders that these indifferent or non-useful characters are often or generally more persistent in heredity than the traits which are plainly adaptive. The slight traits which mark the races of men are in themselves, often not obviously, valuable in the struggle for existence. They are mostly ineradicable in such selective breeding as history offers. In like manner the dusky face, and other marks of Hampshire sheep, persist after the adaptive traits of the original breed have been enormously modified by selection in the direction we regard as sheep improvement. But fine or coarse, fat or lean, Hampshire sheep are still Hampshires.

In Darwin's view, isolation or segregation was doubtless a feature of Natural Selection, not to be set off against the latter as a separate factor in descent. It is very plain from Darwin's own words, as well as from the explicit statement of Francis Darwin, that his main contention was for the reasonableness of the idea of the origin of species through descent with modification. What were the causes of modification, was to him a secondary matter. But he was convinced of the

existence of one such cause, and this one he set forth in most effective fashion. Without selection, the other life-forces known in his day could not be imagined to lead to any evolutionary results. We are to-day in the same condition. If we exclude selection from our category of forces, we imagine an evolution without motive force, an evolution which would bring about no result. But in Darwin's mind, Natural Selection was the cognate of artificial selection. At bottom they were to him the same thing, and segregation a necessary element in both.

Natural Selection was contrasted to supernatural selection or special creation, a theory by which knowable facts were referred to unknowable causes, operations wholly unimaginable in application to details. At present, we have ceased to set off selection as against creation. We agree that all processes are alike natural or alike supernatural, if we consider them in their philosophic aspects.

The origin of a species is as natural as the formation of a snow bank, and both are resultants of forces and conditions within the range of our objective study.

POST-DARWINIAN VIEWS

As compared with Darwin, the investigator of to-day has more facts at his disposal; better instruments of precision; less need to heed the opposition of ignorance and bigotry; and greater

need for analysis of scientific conceptions. Under these conditions, while not departing in essentials from the position of Darwin, we are forced to bring forward isolation as one of the separate factors in the origin of species, and the factor on which the great and growing science of animal and plant geography mainly depends.

Nearly a decade after the publication of the *Origin of Species*, Dr. Moritz Wagner set forth the factor of isolation, and showed in convincing fashion its fundamental relation to the problem of the origin of species.

Wagner showed plainly that in the study of the evolution of any form we need to know where it lived, what it did, how it was bounded, and what was its relation to other forms, geographically as well as morphologically. "For me," he says, "it is the chorology of organisms, the study of all the important phenomena embraced in the geography of animals and plants, which is the surest guide to the knowledge of the real phases in the process of the formation of species."

The work of Wagner, a most necessary supplement to that of Darwin, has never received the attention it deserves. This is due in part to the fact that most of our investigators do not travel. They know little of animal or plant geography at first hand. They have had nothing to do with species as living, varying, reproducing, adapting, and spreading groups of organisms. Another reason lies in Wagner's own attitude of opposi-

tion to Darwinism. He substituted separation, "raümliche Sonderung," for Natural Selection itself, and denied the potency of the latter factor. The two became in his philosophy competing, not coöperating, elements, and this threw on isolation the impossible task of accounting for all the phenomena of adaptation. We may not ascribe to Natural Selection the "Allmacht," or limitless power, which some Neo-Darwinians have ascribed to it, but on the other hand, those who reject it as a factor in organic evolution can give no rational explanation of the universality of adaptive organs and adaptive traits; no clue to the most universal characters of organic nature as it is.

Certain writers urge that neither selection nor isolation are factors in evolution, but rather elements in speciation or species-forming, a process defined as something distinct from evolution. Selection and isolation, as obstacles in the stream of life, help to split the on-moving group of organisms into different categories or species; but the impulse of the forward movement is internal, and the changes of evolution *proper* affect groups as a whole, and are not concerned with splitting them up into species.

This view may be questioned in two ways. It may be untrue as to fact, or it may be a matter of words only. As a matter of fact, we know nothing of evolution *in vacuo,* of progress in life without relation to environment. All forms of

life, we know, are split up into species, with adaptation to external conditions traceable in every structure. We know of no way in which organisms can become adapted to special conditions except by the progressive failures of those not adaptable. Hence we know of no organism which has escaped or can escape from the influence of selection. In like manner, as the world is covered with physical barriers, no organism can escape the form of evolutionary friction which prevents uniformity in breeding. There must be some degree of " räumliche Sonderung," even in a drop of water.

To admit these facts, and yet to say that selection and isolation are not factors in evolution, would appear to make the matter a mere question of words. If by evolution we mean the theoretical progress of life, *in vacuo,* the effects solely of forces intrinsic in organisms, then extrinsic forces or extrinsic obstacles are of course not factors in such evolution. If we mean by evolution, the actual life movements of actual organisms, on this actual earth, then forces and obstacles are alike factors in modifying change, and both speciation and adaptation as well necessary parts of the process.

We admit the primary necessity of variation and of heredity, but we can conceive of no case of actual animal or plant in the forming of which selection and isolation have not played each a large and persistent part. Among the factors

everywhere and inevitably connected with the course of descent of any species, variation, heredity, selection, and isolation must appear; the first two innate, part of the definition of organic life, the last two extrinsic, arising from the necessities of environment, and *not one* of these can find leverage without the presence of each of the others. Isolation as the factor longest overlooked, though to the field naturalist the most conspicuous of the four, must be advanced to the post of honor beside the others, not instead of any of them.

THE CELL IN RELATION TO HEREDITY AND EVOLUTION

BY

EDMUND B. WILSON

I TRUST that my colleagues in this symposium will not suspect me of any intention disrespectful to them if I speak of my own small contribution to it as the voice of one crying in the wilderness. I do not mean to imply by the Scriptural phrase that the cytologist has to announce the coming of a new gospel of heredity or of evolution. He is, to say the least, as much in need of light as are others. I wish only to suggest the somewhat isolated position of the subject assigned to me, dealing, as it mainly must, with matters with which Darwin's own work was not very directly concerned, and which in their detailed aspects belong mainly to the post-Darwinian period. With the notable exception of the provisional hypothesis of pangenesis Darwin made no systematic attempt to correlate his own conclusions with those towards which cell-research was already tending in his day; and pangenesis was rather a speculative construction than an induction from known cytological facts. Nevertheless my intrusion into this circle may perhaps be justified on two grounds. One is the keen interest in the inter-

nal mechanism of heredity everywhere shown by Darwin in his remarkable chapter on pangenesis and attested by many passages in his private letters. The other is the now general admission that the mechanism over which Darwin so long pondered is to be sought in the organization of the germ-cells.

PANGENESIS AND THE PRINCIPLE OF GENETIC CELLULAR CONTINUITY

Of the original hypothesis of pangenesis I shall say but a few words. Darwin says in one of his letters that he had considered it for upwards of five-and-twenty years. It is easily the most abstract and speculative portion of all his writings. It was published against the advice of his trusted friend and counselor, Huxley, who had himself many years earlier written one of the first and ablest reviews of the cell-theory that appeared in our language. Darwin predicted that pangenesis would be called a mad dream; and on its publication the hypothesis was, in fact, received for the most part with hostile criticism or scanty appreciation. In its original form it has been generally abandoned; though one of its principal postulates, remodeled by De Vries to form the hypothesis of " intracellular pangenesis," is still accepted by some biological thinkers. It is none the less deeply significant that so great and sagacious a naturalist, one whose life was so largely given to the study of the external aspects of

heredity and evolution, should have found himself irresistibly driven to look below the surface of these phenomena and should have made so carefully wrought an attempt to picture their physical foundations to his mental vision. His deep-seated conviction that sooner or later the phenomena would have to be attacked from this side is revealed in a letter written to Sir Joseph Hooker, in 1868, where he declares, " I feel *sure* that if pangenesis is stillborn it will, thank God, at some future time reappear, begotten by some other father and christened by some other name." That this prediction still awaits fulfilment need not here concern us. What is significant is the attitude towards the general problem that it reveals. And the modern cytologist, therefore, despite his failure to find support for Darwin's particular conception, has a right to feel that his efforts to analyze the cellular mechanism of heredity would be viewed with sympathetic interest by the great naturalist could he follow their progress at the present time.

Pangenesis was put forward many years after Virchow had pronounced his celebrated aphorism *" Omnis cellula e cellula"* (which Darwin quotes), and a full decade after the eminent German pathologist had insisted on the " eternal law " of genetic continuity by cell-division. Darwin nevertheless admitted this law unreservedly only in the case of plants, and went no further than to recognize its wide prevalence among ani-

mals. In both cases he assumed that in addition to the powers of division cells multiply by means of minute germs or "gemmules," which are thrown off by the somatic cells, collected from all parts of the body to form the sexual elements, and are "ultimately developed into units" (cells) like those from which they were originally derived.[1] Pangenesis thus comprised two principal postulates, both of which had been in a measure foreshadowed by the speculations of Bonnet, Buffon, and even earlier writers. One is the particulate or meristic assumption that particular hereditary traits are represented in the germ-cell by discrete and specifically organized particles, the "gemmules" or "pangens," that are capable of self-perpetuation by growth and division without loss of their specific character. The second assumption is that the gemmules are cell-germs originally produced by the somatic cells; and by this Darwin sought to explain the transmission of somatogenic or acquired characters. How have these two assumptions fared with the progress of modern studies on the cells?

[1] The development of the gemmules was supposed to depend on their "union with other partially developed or nascent cells, which precede them in the regular course of growth." Darwin does not make it quite clear whether he assumed that the gemmules actually grow into new cells. Many passages (like the one placed in quotation marks in the text above) seem open to no other interpretation; but in the case of plants, accepting the universality of division in them, he concluded that "the gemmules derived from the foreign pollen do not become developed into new and separate cells, but penetrate and modify the nascent cells of the mother plant." This process, he says, is almost identical with a fertilization of the cells of the mother plant by gemmules derived from the foreign pollen.

The first has been accepted by many acute biological thinkers as almost a logical necessity, and has been developed, especially by Weismann, into one of the most ingenious and elaborate speculative constructions to be found in the whole history of biology. Its logical grounds need not here be analyzed. I will only emphasize the fact that the conception did not grow out of actual studies on the cell, but was an imaginative construction, based on the facts of variation and heredity. It may be true; but for the present we can only regard it as a kind of symbolism, analogous in some respects to the molecular-atomic symbolism of physical science, but of far more doubtful validity. Those who find such a symbolism useful will encounter no positive obstacle in the known cytological facts—they may even find in them a certain amount of indirect support—but the assumption remains unverified, and is probably unverifiable.

The second postulate of pangenesis is wholly unsupported by either experimental or cytological evidence. There is not a particle of evidence to show that in the higher forms of life cells produce gemmules or that the germ-cells are built up by the aggregation of such bodies derived from the somatic cells. The most fundamental contribution of cell-research to the theory of heredity is the law of genetic continuity by cell-division. Cells arise only by the division of preexisting cells. And the stream of growth and

division by which the continuity of organization is maintained seems clearly enough to be genetically irreversible. It flows forward from germ-cell to germ-cell in endless succession. It is periodically diverted from the germ-stream to form the bodies of successive generations of individuals. These are made of the same stuff as the stream from which they flow. In each generation the germinal stuff runs through the same series of transformations; hence that reappearance of the same traits in successive generations that we call heredity.

This conclusion loses nothing of its force by reason of the fact that in a sexual reproduction or regeneration the whole body may be reproduced from a fragment, from a small group of cells, or even from a single cell, of the soma. These cells, too, have arisen by division in unbroken descent from the germ-cell; they, too, have been made from the same original stuff; and they, too, hand on by division to their descendants the specific tradition of their lineage. It is true that these cells and the germ-cells alike grow by the intussusception of matter from without, that the cell-substance is built from, and its activities modified and controlled by, materials that have been elaborated by other cells. But the whole force of the evidence goes to show that their fundamental basis is determined by genetic continuity with that of their predecessors, that something is handed on by division which holds

the cell true to its specific type and builds the incoming food-stuffs into the characteristic fabric of the species. I need not dwell on a conception with which we are all so familiar. Some of the specific applications of the doctrine may have proved unacceptable, but the advances in our knowledge of the cell are ever adding weight to the fundamental principle of germinal continuity for which so many eminent investigators, from Remak and Virchow to Nussbaum and Weismann, have contended. And this principle obviously affords the true standpoint from which the phenomena of heredity and development must be viewed.

From this standpoint we are confronted with four principal questions, which I shall in the briefest possible way attempt to consider. (1) What is the physical basis of heredity? (2) How is it transmitted from cell to cell? (3) In what way does it play its part in the determination of the hereditary characters? (4) How may it be so modified as to give rise to new heritable characters?

THE PHYSICAL BASIS OF HEREDITY

It is now universally admitted that the physical basis of heredity is contained in the germ-cell. Is this basis formed by the entire living energid, or may we distinguish in the cell a particular species-substance or idioplasm, that is at least theoretically separable from the other cell-con-

stituents? This question has not yet been answered with certainty. The cell-system forms an enormously complex moving equilibrium, which must in one way be regarded as a single and indivisible unit. From this point of view it may justly be maintained that the basis of heredity and of the vital activities generally is represented by the cell-system in its totality. But such a position, philosophically correct though it may be, cuts us off from the possibilities of exact analysis. We have every right to inquire in what way the energies of cell-life are distributed in the system and how they are related; and the question whether certain elements of the system may possess an especial and primary significance for the determination of the cell-activities forms a legitimate part of this inquiry.

I stand with those who have followed Oscar Hertwig and Strasburger in assigning a special significance to the nucleus in heredity, and who have recognized in the chromatin a substance that may in a certain sense be regarded as the idioplasm. This view is based upon no single or demonstrative proof. It rests upon circumstantial and cumulative evidence, derived from many sources. The irresistible appeal which it makes to the mind results from the manner in which it brings together under one point of view a multitude of facts that otherwise remain disconnected and unintelligible. What arrests the attention when the facts are broadly viewed is the unmis-

takable parallel between the course of heredity and the history of the chromatin-substance in the whole cycle of its transformation. In respect to some of the most important phenomena of heredity it is only in the chromatin that such a parallel can be accurately traced. It is this substance, in the form of chromosomes, that shows the association of exactly equivalent maternal and paternal elements in the fertilization of the egg. In it alone do we clearly see the equal distribution of these elements to every part of the body of the offspring. In the perverted forms of development that result from double fertilization of the egg and the like it is only in the abnormal distribution of the chromatin-substance by multipolar division that we see a physical counterpart of the derangement of development. Only in the chromatin-substance, again, do we see in the course of the maturation of the germ-cells a redistribution of elements that shows a parallel to the astonishing disjunction and redistribution of the factors of heredity that are displayed in the Mendelian phenomenon.

These are perhaps the most striking of a multitude of facts that point towards the chromatin as the embodiment of specific *primordia* of determination. We may be sure that the microscope reveals to us but part of the story; but that which we see is not for this reason less significant. Experiment has taught us, it is true, that the rôle of the nucleus in determination cannot be regarded

as an exclusive one. It is certain that specific factors of determination also exist in the protoplasm of the egg; it is possible that the same may be true of the spermatozoon. Experiment has demonstrated in the clearest manner that many features of the early development, among them some of the most important, are immediately determined by conditions in the egg-protoplasm without direct action of the nucleus. But this fact can be rightly estimated only when the whole genesis of the egg has been taken into account. The researches of recent years have proved that the egg undergoes a long process of development during its ovarian history and in the process of maturation, in the course of which the greater part of its protoplasmic substances are formed and ultimately segregated in a particular configuration. It has thus become more than probable that some at least of the determinative conditions in the protoplasm of the fertilized egg are of secondary origin—that they are the outcome of an antecedent development in which the nucleus has played its part. Important formative protoplasmic materials are known to be of nuclear origin. It is possible that all may have such an origin. But even if we do not go so far as this, even if we admit that the determinative factors of the nucleus constitute but one element in an activity that properly belongs to the living energid as a whole, we still can not close our eyes to the plain record that is written in the history of the nuclear

substance. I doubt whether any one holds the view, which some of the opponents of the chromatin hypothesis have endeavored to force upon its adherents, that the nucleus enjoys a complete "monopoly of heredity." To what extent the chromatin embodies primary factors of determination remains to be shown by further research. We are still too ignorant of the physiological relations of the nucleus and cytoplasm to be justified in any attitude of dogmatism on this question. But as a matter of evidence the conclusion that chromatin does embody such factors seems at least a probable one. As a means of practical inquiry it is, I believe, a good working hypothesis, without which we should be deprived of one of our most effective instruments for the analysis of the mechanism of heredity. And recent research has, I think, clearly shown that, far from being exhausted as some of its critics would have us believe, this hypothesis is steadily opening new possibilities of inquiry.

CELL-DIVISION

Accepting the idioplasm hypothesis, in the sense I have indicated, what do we know of its mode of transmission? We may answer with assurance that it is transmitted from cell to cell by division; and we may still safely assume, I think, in most cases by mitotic or karyokinetic division, though the direct or amitotic process may play a larger rôle than was formerly supposed.

We can but glance at one or two of the most significant features of karyokinetic division. The most striking and telling of these is the contrast so often shown between the distribution of the nuclear and of the protoplasmic elements. With certain exceptions in the phenomena of maturation, which only bring fresh support to the general principle, nuclear division is both quantitatively and qualitatively exactly equal. Protoplasmic division is often both quantitatively and qualitatively unequal, separating substances that have been proved by precise experiment to be of different physiological value. But more than this, the formation and division of chromosomes effect not merely a mass-division of the chromatin but an equal meristic division of its whole substance; and as Wilhelm Roux first urged, we can find no meaning in the whole elaborate process if the chromatin be not composed of qualitatively different elements that require equality of distribution. That such is really the constitution of the chromatin can no longer be doubted by any who are familiar with the evidence. If the chromosomes be not actually persistent individuals, as Rabl and Boveri have maintained, they must at least be regarded as genetic homologues that are connected by some definite bond of individual continuity from generation to generation of cells. And the evidence has steadily accumulated to show that the chromosomes exhibit definite qualitative differences. In many animals and

plants constant differences of size, in some cases also of form, are shown among the chromosomes. Specifically different classes of chromosomes can in some cases be distinguished, which show constant and characteristic peculiarities of behavior in respect to some of the most important operations of the cell. The probability is increasing that individual chromosomes possess a particular significance for the development of particular characters. It has become probable that sexual dimorphism in general is determined by a difference of nuclear constitution between the sexes. In some groups of animals the sexes differ in respect to one or more particular chromosomes. In a more general way, Boveri's experiments have proved that abnormal combinations of chromosomes lead to falsified forms of development; and these observations give the strongest reason to believe that normal development is dependent upon the normal combination of the chromosomes.

All these facts are pointing in the same direction. They render the conclusion almost irresistible, not only that the chromatin-substance is involved in heredity, but that the chromosomes are composed of specifically different materials, the *ensemble* of which is essential to normal development. It is obvious that the beautiful mechanism of karyokinesis is perfectly adapted for the meristic division and equal distribution of these materials. The energies that lie behind the for-

mation and action of the karyokinetic figure constitute a puzzle for which, as it seems to me, no adequate solution has yet been found. But the effect of its action gives us good reason to regard it as the most important instrument by which the nuclear substance is handed on with its integrity unimpaired from generation to generation of cells.

DIFFERENTIATION

Our third question involves the problem of differentiation, which is inseparable from that of cell-metabolism in general, since it involves the mode of interaction of nucleus and protoplasm. It is a significant fact that visible structural differentiation affects the protoplasmic substance in far greater degree than the nuclear. Both in their structure and in their modes of activity the most important characteristics of different kinds of cells are found in the protoplasm. To some extent, no doubt, the nuclei of different tissues show certain characteristic peculiarities, and these can in a measure be correlated with the function of the cells. It is nevertheless obvious that the most characteristic features of the muscle-cell, the nerve-cell, or the gland-cell are displayed in the protoplasmic rather than the nuclear substances. And this again falls into line with the view that the nucleus is the main conservative element of the cell-system, the protoplasm the plastic element through the modifications of

which the cell adapts itself to the performance of the varied special conditions of cell-life.

In considering the problem of differentiation we are therefore led to inquire in what manner the nucleus may be conceived to operate in the determination of specific modes of protoplasmic change. De Vries and many of his followers have supposed that control of the cell is effected by an actual migration of organized gemmules or pangens from nucleus to protoplasm. But do we really need to employ the pangen symbolism in the consideration of this question? It seems a sufficient basis for our practical attack on the problem to assume that the control of the cell-activities is at bottom a chemical one and is effected by soluble substances that may pass from nucleus to protoplasm or from protoplasm to nucleus. Certainly it is to such a view that very many of the chemical and physiological studies in this field are now unmistakably pointing. The opinion is gaining ground that the control of development is fundamentally analogous, perhaps closely similar, to the control of specific forms of physiological action by soluble ferments or enzymes. Experiment has established the fact that certain forms of development are thus controlled by substances, the "hormones," that may be extracted from the cells that produce them, and upon injection into the body call forth their characteristic results. Such an effect, for instance, is the development of the cock's comb in the hen

upon injection of testic-extract and its recession to the characteristic female condition upon cessation of the injections, as recently described by Walker. Analogous phenomena are seen in the well-known effects of thyroid extracts, or in the effect upon the mammary glands of injection of extracts of the fetus, as described by Starling and Lane-Claypole.

We are thus led to something more than a suspicion that the factors of determination, and therefore of heredity, are at bottom of chemical nature. It is a well-known fact that corresponding tissues of different species often show characteristic chemical differences; and to some extent the same is known to be true of the germ-cells. The conclusion thus becomes highly probable that the characteristic differences of metabolism between different species, including those involved in development, are traceable to initial chemical differences in the germ-cells. In so far as the chromatin theory expresses the truth, the primary basis of these differences may be sought in the nuclear substance. There is good reason to believe that some at least of the enzymes are of nuclear origin. It seems a promising hypothesis that the chromosomes may be regarded as self-perpetuating magazines of specific substances, similar in nature to the enzymes or their chemical antecedents, that play an essential rôle in the determination of the cell-activities, including those involved in development. From this

point of view the fertilization of the egg might almost be compared to an intracellular injection of enzymes.

The apparent simplicity of such an hypothesis should not delude us into the belief that it touches the root of the matter. It presupposes a specific "organization" of the chromosomes of which we know nothing, and upon which must depend the perpetuation of their characteristic chemical constituents. In this direction we are thrown back upon purely speculative constructions which it would be unprofitable to follow out here. But so far as the hypothesis goes it seems to offer a really practical point of attack for the chemical study of differentiation and heredity. In the Mendelian phenomenon we see a synthesis, splitting apart, and recombination of determinative factors that is singularly like that of chemical elements or radicals. In the Mendelian heredity of color, for instance, the orderly resolution by the germ-cells of compound pigment-producing factors into simpler ones, their recombination to form new compounds, the intensification or dilution of color by specific and separable factors, the production of particular colors by mixing together factors which are singly incapable of producing color—in all this we see a series of operations that show an astonishing similarity to the procedure of the chemist in his laboratory. That such things are possible in the case of relatively simple characters, such as colors, gives strong

ground for the belief that similar operations are concerned in the production of more complex characters. Those who hesitate to draw such a conclusion may well reflect upon the remarkable effects of the "internal secretions" of the enzymes and hormones, and upon the extreme susceptibility of the developing embryo to even very slight chemical changes in the surrounding medium. It is my belief that in the direction here indicated lie the greatest possibilities of future investigations upon the cell, and that in the union of cytology and biochemistry lies our greatest hope of future advance.

HEREDITY AND EVOLUTION

Lastly, if we accept the working hypothesis that the *primordia* of determination are chemical in nature, how may we conceive them to be so modified as to produce new characters? It seems to me that this question may well be reversed; for the wonder is, not that the idioplasm changes, but that it adheres so stubbornly to its type. It may as well be admitted that both our cytological and our chemical knowledge in this direction is practically *nil.* It is well, further, to speak a word of caution at this point. We must not forget that some of the most acute and thoughtful of naturalists have in recent years expressed the conviction that the ultimate control of development is not to be sought in the physico-chemical properties of the germ-cells, but in an indwelling

"entelechy" or "élan de la vie," a power of unknown nature, that may, in the last analysis, be psychical in nature. But, profoundly interesting as some of these vitalistic speculations are, we are bound to hold fast to the physico-chemical and mechanistic hypothesis of heredity until the possibilities of observation and experiment in this direction have been exhausted. If there be a physico-chemical basis of heredity we should expect to find it capable of modification by physico-chemical agencies; and so much, at least, is known to be the fact. It has been abundantly demonstrated that both the body-cells and the germ-cells react to changes of the environment by definite physiological and morphological changes. Many experimenters have demonstrated the extreme susceptibility of the discharged eggs or spermatozoa to even very slight chemical and physical stimuli. We can not doubt that they are equally sensitive to stimuli while still within the body, and at every stage of their development. The almost unique experiments of MacDougal on the higher plants seem to show that direct chemical treatment of the germ-cells may produce definite and irreversible effects upon the offspring. Those of Tower on the insects, though less direct, are hardly less convincing.

Though we may not fully understand the manner in which the germ-cells are modified, there is no inherent improbability or difficulty in the conception that such modifications will produce blas-

togenic variations or mutations that are inherited, permanently or temporarily. We can readily understand that the constitutional effects of temperature, food, moisture, and similar general agencies of the environment may manifest themselves in definite changes that reappear in following generations because the germ-cells have been directly affected in the same way as the somatic cells. It is natural to suppose that the idioplasm possesses a slight instability of chemical or molecular composition that results in corresponding fluctuations or indefinite variations of the adult, which may or may not be inherited. We find no difficulty in the conception that the idioplasm may undergo considerable, sudden, and irreversible changes which produce mutations of greater or less degree. We can comprehend how particular constituents of the idioplasm may change without affecting others, thus giving rise to mutations in respect to only a single character or a particular group of characters. We can conceive the idioplasm as undergoing a slow secular change that results in continual divergence in many directions or in a definite orthogenetic line of transformation. But in respect to the transmission of acquired characters the old difficulty confronts us to-day as formidable as when it was first fairly revealed to us through the argument of Weismann. What is really difficult to comprehend, what I think we can not really conceive if pangenesis be discarded, is how the idioplasm,

or the germ-cell as a whole, can be a storehouse of specific and detailed somatic impressions which cause the reappearance of similar somatic effects in generations to come.

Darwin's ingenious attempt to picture such a process was a legitimate speculation, worked out with a power and insight that should stir enthusiasm in even the most skeptical of critics. More than this, it still remains, as I think, the only intelligible hypothesis of the transmission of acquired characters, as Darwin understood the phrase. But it finds to-day little or no real support in the results of observation and experiment. Attempts have been made to substitute for Darwin's migrating gemmules soluble internal secretions—hormones or other substances—that are produced by the various organs and transmitted to the reproductive organs through the fluids of the body. Heredity has been compared, and with justice, to an "organic memory"; and this has been assumed to be a property of the organism as a whole, irrespective of the distinction between germ-cells and soma. It has been urged that the heredity of acquired characters is more readily conceivable if the increments of change be small and extended through long periods of time. Any or all of these things are possible; but let us not deceive ourselves. Does any of these assumptions really lessen the difficulty or give us a clear mental picture of what must occur if the heredity of acquired characters be a fact?

I do not see how. Inability to form a clear *a priori* conception of the process has in itself no validity as an argument against the fact, if fact it be. The progress of biological discovery has repeatedly transformed apparent *a priori* impossibilities into everyday realities. And if experiment shall really demonstrate the transmission of somatogenic modifications the cytologist has no fundamental obstacle to interpose. The mechanism that his studies have revealed will account for the transmission of all forms of germinal modifications, however they may be caused. The question involved is not of the transmission of the idioplasm or of the germ-cell, but of its interaction with the soma; and this is not an *a priori* question, but one of fact. Let us admit freely that such an interaction as Darwin assumed may be a real and potent factor in heredity, though it gives no hint of its existence in the visible apparatus of the cell. In the present defective state of our knowledge we may well grant that there may be many a thing between germ-cell and body that is not yet dreamed of in our biological philosophy. But has the transmission of acquired characters, in the strict and proper sense of that much abused phrase, been demonstrated? If in closing I venture to question this, I pray that my sins be not visited upon the study of the cells, but upon a failure to discover the demonstration in other fields of inquiry.

THE DIRECT INFLUENCE OF ENVIRONMENT

BY

D. T. MacDOUGAL

Any serious consideration of the diversity of organisms, of the complexity of the qualities they bear, of the relationships they sustain, and of the character of the stresses under which they exist with relation to the environmental setting, leads inevitably to the conclusion that their evolutionary development must have been affected by many modifying agencies; that the origination, or activation of their qualities or characters may not be ascribed to any single causal force or guiding factor; and that the course of heredity from generation to generation has been determined by many things beside the simple inertia of primitive initial qualities of protoplasm.

When we join in the accepted generalization that the qualities and forms of organisms now existent are the net result of the action of environic forces upon ancestral structures, selective as well as initiatory, we implicate a much larger group of conceptions than that embodied in the present thesis, since it is the intention to confine discussion to the possibilities that arise when liv-

ing or self-generating matter transmits its specialized characters from one generation to another in the germ-cell, and displays its periodic somatic expansions in ontogeny.

Within this definite and restricted field, exactness and clearness of comprehension of the relations involved will depend directly upon the thoroughness with which we may be able to connect our conceptions with the physico-chemical processes of organisms.

The more important external, direct, or physical factors, the influence of which induces adjustments and engages the activities of protoplasm, include radiant energy in its various phases, and the chemical structure of the medium, substratum or substances coming into contact with the living matter and included with its intake and output. These agents interlock intimately with the parts of the self-generating protoplasmic machine, furnishing building material, energy in various forms, catalysts, and control reactions in a manner so intimate that it is impossible to think of living matter free from its environic setting.

Now if we set about the calibration of the quantitative relation of any of these factors to living matter, or attempt an estimation of the qualitative effect, we will find that, with respect to any given strain of organisms or any individual, the constellation of specific activities, processes or functions, grouped in the plant are adjusted in such manner that they proceed at the most advan-

tageous rate with relation to each other within, for example, some narrow range of temperature. In our easy acceptance of the obvious, we are apt to assume that these optimal conditions are furnished by the native habitats of plants, or in other words, the place they happen to occupy in their movements about the world when they are called to our attention. Now, on the one hand, plants simply are found in areas they have been able to reach, and "native habitats" may by no means offer the optimal conditions, a condition of affairs of which more than a hint is furnished by the irruption of weeds, followed by a development of a vigor unknown within the previous range of the species. On the other, the reminder is necessary that no one habitat may furnish the optima for the accomplishment of all of the processes involved in the ontogeny and reproduction of the individual, and all environic relations include groups of compromises and of adjustments that put the capacity of the living matter to the utmost stresses it may bear.

Two main considerations arise when attention is directed to the behavior of the organism as it encounters the external factors in unusual intensities, an experience which has been countlessly repeated and which is one of the eliminating factors in selection. The first concerns the mechanism of the adjustment of the individual to altering environment, and the second, the possibilities of transmission of the effects of the adjustment

to the progeny, both in functional capacity and accompanying structure.

ADJUSTMENT OF THE INDIVIDUAL TO ALTERING ENVIRONMENTS

Let us take, for example, a plant standing in the open in a habitat in which it is firmly established, and introduce some modifications of wide range of the insolation, which may or may not register with anything previously encountered by this individual. The primary or direct effect of the change will undoubtedly be a modification of the reaction-velocities of some of the chemical processes so that metabolism and all of the life-phenomena dependent upon it will undergo alterations in rate, cell-division, chromosomatic involution, catalyptic action involving respiration, intake and excretion, and finally growth also. A secondary effect accompanying these changes will be due to the irritability of the living matter by which sudden changes in almost any external factor will exercise a releasing or unloosing action. Outward manifestations of such action are seen in the various thermotropic and heliotropic movement of leaves, and while there seems to be a disposition on the part of some physiologists to eliminate metabolic activities from the realm of irritable reactions, yet it does not seem justifiable upon present evidence.

Whether an irritational phase intervenes or not, when an environmental factor undergoes

rapid alteration, the activities affected soon assume a fairly steady rate, determined directly by the reaction velocities of the substances concerned, and the change goes no further than that of a purely physiological, or, strictly speaking, physico-chemical, accommodation. If the change in question is introduced in the developmental period of the individual, the members and organs not fully mature may take on unusual structures and assume aberrant or variant forms, while if the resting seed or spore is germinated under altered conditions, all purely irritational responses are eliminated and the entire individual may show a more or less atypic ontogenetic procedure.

This somatic variability in response to environment is a matter of common observation, but deviations of this character are of but little importance in heredity unless they or their effects are repeated in successive generations. This transmission of somatogenically induced characters is the cause of our confusion and the source of our doubts, constituting as it does the essence of the controversy as to the " heredity of acquired characters." On the one hand Weismannists predicate an isolated current of heredity coursing from germ-cell to germ-cell, yielding qualities that direct ontogeny, but receiving nothing in return except nutrition and continuance, while on the other hand a by no means voiceless constituency presses for the acceptance of the conclusion that

every wave of variability and every impress of the environment upon the soma are communicated from it to the germ-plasm upon which it becomes forever indelibly engraved. When to this claim there is added the assumption that while the effect of a single external impression may be very slight, its repetition, rhythmically or otherwise, would finally cumulate to produce appreciable and lasting effects, we have a conception difficult to prove or disprove, especially since it is a well-established fact that repetition of stimulation does give cumulative effects in both irritomotility and variability. The whole question, however, resolves itself into the comparatively simple inquiry as to the physiological connections and correlations of the soma and germ-plasm.

It is well known that not all of the various organs or tracts of tissue are directly affected alike by any external factor, a result due to the essential differences of the cells composing them. Thus an arid atmosphere or intense insolation would affect leaf activities chiefly, while unusual soil concentrations would influence roots only. The various members of the root and shoot are in close correlation, however, and the activity, growth, and mode of development of organs not directly acted upon by the factors mentioned may be profoundly influenced by the altered products of the organs that are affected. Thus the wounding of a root is reflected by changes in the shoot, the removal of one of the parts of a compound

leaf causes adjustments in the remaining ones, and instances might be multiplied almost indefinitely to show that effects produced in one part are quickly and forcefully transmitted to other parts of the soma. It matters not for the present whether the means of communication be special tracts, nervous mechanisms, chains of catalytic reactions, or what other method of communication.

THE ACTION OF SOMA UPON GERM-PLASM

Similar communications between the egg and soma are to be encountered. In some of the carpotropic and gametropic movements of seed-plants, the accomplishments of definite stages in the development of the embryo-sac and fertilization, result in impulses to stems and peduncles several centimeters distant, producing movements and morphogenic alterations of a very striking character. Without further enlargement on this theme it is to be said that the securest foundation is laid for the conclusion that well-defined correlations exist in the plant by which secondary effects of the action of external factors, or of morphogenic or embryonic procedure, may be freely communicated from one part of the soma to another, and from the egg to the soma.

With such a substantial substratum of established facts, we now turn to the problem as to the communication of effects from the soma to the

egg or sperm, in such manner that these effects would be transmitted to succeeding generations.

The most obvious and the most primal relation between the soma and the egg is the nutritive one, and a review of the evidence offered by Pictet and others leads to the conclusion that the character of the building material supplied to the egg as varied by environmental influences may work changes that pass from one generation to another, so that it is indubitably established that the egg is not isolated and possessed of such highly developed selective power that it may avoid the intrusion of unusual substances.

The experiments of Oscar Riddle, S. H. and S. P. Gage,[1] in which it was shown that Sudan III, a dye, fed to a hen, results in the coloration of the yolk of her eggs, and that the chicks hatched from such eggs take up the dye from the yolk, which finds a lodgment in their own fatty tissues, are of special interest in this connection.

Actual available evidence does not warrant us in predicating any other form of influence of internal region upon the germ-plasm as it takes form and special activity in the egg and sperm, beyond that of physio-chemical processes originating in the soma. Alterations in these processes which might affect the egg and be registered in its hereditary activities might occur at any stage of the ontogeny without direct reference to the time intervening between the reception of the

[1] *Science*, 28: 494. 1908.

stimulus and the reception of a possible impress by the egg.

Concerning the results from repetition of stimuli in a series of generations, about the only facts at hand are those obtained from a study of variability as affected by nutrition, in which it is found that more favorable conditions of nutrition increase the range, and that further increases accumulate with the continuance or repetition of the optimal conditions with relation to successive generations. The foregoing may be taken as a fair representation of the physiological basis of the possibilities by which alterations in the soma might be impressed upon the germ-plasm and transmitted to successive generations, and a description of the authenticated observations and well-ordered experiments which have been made by skilled workers in dealing with this subject during the last few decades would form no mean record. It would entail a historical review far too voluminous for the present occasion. However, among other general features it appears that plants moved to habitats and to cultivated fields to the northward and southward have been seen to take on a seasonal rhythm in accordance with the new climatic conditions encountered. Unusual temperatures and foods have caused marked alterations in structure, markings, composition of the body, periodicity of reproduction and range of adjustment and endurance in both plants and animals, but in all of these cases the

alteration gradually disappeared when the inducing conditions were removed, except in a few instances in which it could not be demonstrated that the germ-plasm had not been directly affected.

Butterflies, moths, fishes, crustaceans, birds, guinea pigs, rabbits, trees, fungi, cereals, and bulbous plants have all been drawn into the experimental field with a remarkable unanimity of negation in so far as the somatogenic induction of characters was solely concerned, which might be fully transmissible to successive generations not under the influence of the exciting factors. Temperature, light, food, and composition of the medium or substratum all have been tested in their various effects. Only when the germ-plasm has been acted upon simultaneously with the soma has any well-defined reappearance of induced characters in succeeding generations been noted, and of the earlier results those of Standfuss and Fischer seem most notable, since in experiments with *Vanessa* and *Arctia* the application of special temperatures or the modification of nutritive conditions induced the formation of aberrant characters in some of the offspring. The new qualities were displayed in varying degree, and maintained their distinctive appearance in the products of hybridization with the parental strain. There seems to be some doubt among zoölogists acquainted with these forms as to the significance of these results. It is not clear as

to the manner in which the formation of the new characters was induced. The experimental agencies employed affected both the soma and the germ-plasm segregated in the reproductive elements, and no interpretation of the facts would justify the conclusion that the aberrant qualities were somatogenically acquired.

While failure has attended all efforts to demonstrate the continued inheritance of impressions received by the body alone, a number of arrangements are found in nature which seem to demand such action for their explanation. Among these certain rudimentary organs, and also co-adaptations in which simultaneous specialization occurring in two or more members of the body has made for increased fitness, are difficult of interpretation without the interposition of somatic induction.

DIRECT STIMULATION OF THE GERM-PLASM IN BEETLES

Meanwhile the possibility of influencing heredity by agencies acting directly upon the germ-cells has awakened the keenest interest among biologists. The relations of soma and germ-plasm make it difficult to induce changes in the body without affecting the reproductive elements, while it is possible to devise experimental methods by which the egg or sperm alone may be subjected to modifying agencies. This has been done with such success that some very important

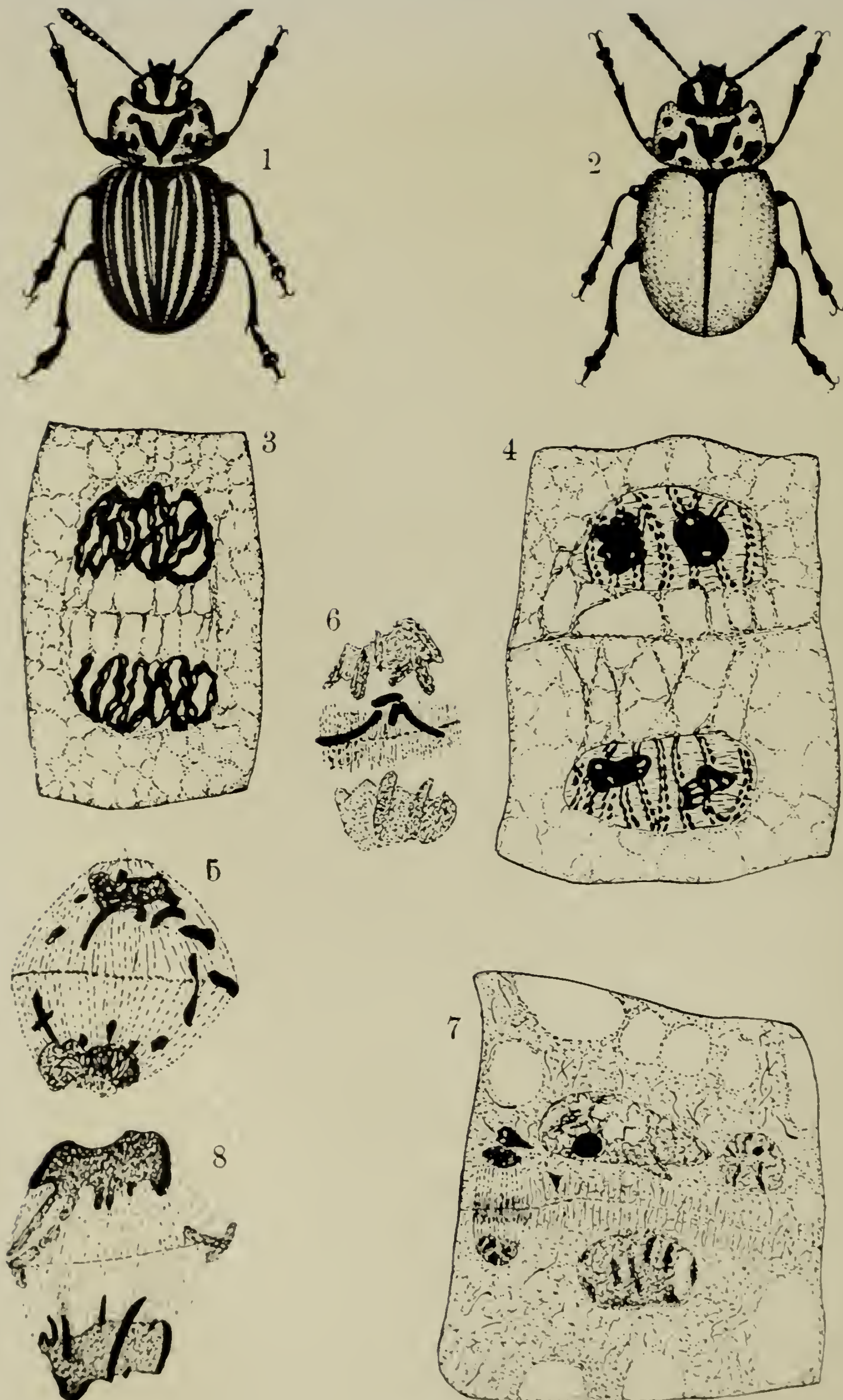


PLATE I.

Fig. 1. Leptinotarsa undecimlineata, normal form.

Fig. 2. Form derived from L. undecimlineata through the application of the climatic conditions. For convenience this form has been called angustovittata because it most closely resembles a species described by Jacoby, but it differs from angustovittata in many characters considered important by the systematists. [From Plate 16, Investigation of Evolution in Chrysomelid Beetles of the genus Leptinotarsa. Carnegie Institution, Publication No. 48, 1905. After Tower.]

Figs. 3, 4. Normal mitosis of nuclei in cells of plant.

Figs. 5, 6, 7, 8. Irregularities of mitosis in cells of onion roots resulting from exposure to radium. [After Gager.]

conclusions may be founded upon the evidence obtained. The results of the work by Tower, in which beetles of the genus *Leptinotarsa* were subjected to various combinations and alterations in climatic conditions in a series of experiments carried on for a period of more than twelve years, have recently been available and far surpass in importance anything previously obtained from animals. The value of the evidence is greatly enhanced by its repetition, by the fact that pedigreed cultures were used and conditions so regulated that an accurate analysis of the effects of the various climatic factors could be made.

Professor Tower finds that:—

"Not only members of the genus Leptinotarsa, but also of allied genera can be directly modified by the application of intense environmental stimuli to the germinal material. The use of temperature and moisture in unusual degrees of intensity has given rise to a number of forms and modified characters. Some notion of the extent of these modifications is gained from the two following illustrations. In Plate I, Figure 1, is shown the normal form of *L. undecimlineata*, and in Figure 2, a race derived from it by the application of low temperature and low relative humidity. This new form resembles in some respects Jacoby's species *L. angustovittata*, and breeds true. It matters not whether this new form is a species, race, elementary species, or a nightmare to the systematist, the important point is, that as the result of subjecting the germinal material to certain conditions at a fixed point in its development, that the eggs thus treated, when fertilized by normal male germs, gave the form shown, which breeds true without subsequent segregation of charac-

ters. In this case both structural and color characters are modified.

"Many other illustrations might be given of the entire change in the coloration of body, both in larvæ or adult, of the modifications of parts and of particular portions of the body or of individual color marks. These arise, some from the treatment of the male germinal material, some from treatment of the female germinal substance, others from a treatment of both germinal materials to the conditions of experiment. In some of the modifications thus induced, the full expression of the change is attained at once in the individuals that develop from the treated germs, and in others it requires one, two, three or more generations to attain the full expression of the modified attribute. It does not make any difference whether the full development of the modification is attained at once, or after the lapse of several generations, the behavior is the same, in that there is no regression or reversion to the parental condition.

"In my published work I have given some of the results derived from the application of external factors at one stage of the germ cells. Eggs that have been subjected to the conditions of experiment immediately before the maturation period, have given the results now in print and it was from eggs so treated that the race illustrated in this statement came. Analysis of the results from these experiments shows a number of interesting points.

"First: Not all of the germ-cells are modified, but only a varying proportion of them, which may indicate one of two things; either that there are differences between the eggs in their capacity for modification, or that only certain eggs were in the proper stage for modification, at the time of the application of the experimental conditions. Second: The results are sometimes modifications all in one direction, at others they are in many directions, two, three or more different forms arising from the same experiment. Third: The mod-

ifications in some characters stand apart from the condition of the parents without intergrades, at other times the same modifications have intergrades; some characters, as far as known, never have intergrades and some always show them, and there is no place where one can draw a line and say that on one side all are discontinuous variations and on the other side they are continuous. Fourth: The modifications produced never, as far as known, segregate the characters in subsequent generations, indicating a condition different from hybrids. In this respect my results are like those of MacDougal with plants."

Obviously the subjection of an entire organism to the influence of an enveloping factor implies also its action upon the soma as well as upon the germ, and while necessarily the possibility of some secondary or parallel inductions are not entirely eliminated, yet an examination of the detail of the experiments points unerringly to the conclusion that the major effect is due to the action of the external agency on the egg or sperm. The soma is indeed the most immediate environment and medium of the germ-plasm, and its activities must interlock most intricately with those of the egg and sperm, in what manner has already been suggested.

EFFECT OF RADIATIONS ON GERM-PLASM

Somewhat easier of analysis are the effects produced by such forms of energy as radiation of known character and measured wave-length as illustrated by the results secured by the use of X-rays, Roentgen rays, and radium emanations.

In general it may be said that such forms of energy retard growth and compel an incomplete differentiation of tissues when applied to an individual before maturity, producing serious deleterious effects if applied afterward. When eggs or sperm are treated by these agents, the most profound disturbances may ensue in the primary divisions, and the ontogeny of individuals arising from a fertilization, either component in which has been subject to such action, shows a destruction of correlations and great disturbances in symmetry, according to the most recent tests of MacGregor with frogs. In most of these cases the disturbances were so great that the individuals concerned were incapable of reproduction, and nothing further concerning their effect on heredity was possible. The fact that the results were of the same general character, whether the egg or sperm was subjected to the action of the experimental agency, whether held in the reproductive tracts of the animal or wholly free, is a matter of some importance, since it eliminated the intervention of the soma as a possible source of modification of the results.

Recently Dr. C. S. Gager has completed an extensive study of the influence of radium on plants so applied that the elements subjected to its action survived and were capable of reproduction. An examination of the effects on the nucleus as well as the structure of the soma was made with some highly interesting results.

When the root tips of the onion (*Allium cepa*) were exposed for different periods of time to rays from radium bromide of various degrees of activity, profound alterations were induced in the mitoses of the cells. In nearly all cases the passage of the chromosomes to the poles of the spindle proceeded with great irregularity. Frequently one or two chromosomes would remain behind near the equator of the spindle, failing completely to take part in the organization of the daughter nuclei (Plate I, Fig. 6). At times several chromosomes or portions of chromosomes would remain at one side of the spindle, or be carried beyond the poles (Fig. 8), or again be drawn out as if subjected to considerable tension (Fig. 5). In one instance, after the main cell-division was nearly completed, a small secondary spindle, in tardy telephase, was observed at one side of the cell (Fig. 7).

From these results it was seen that the radium treatment afforded a method by which chromatin elements might be eliminated from reproductive cells, and if these are the carriers of certain specific characters, as indicated by the researches of Wilson, then a ready means of suppression or substitution of characters would be afforded. In addition to these distinctly radical effects, the chromatin might be modified so as to form the basis of characters not hitherto expressed by the organism.

Proceeding on this basis, Gager exposed to

radium rays the egg and sperm-cells of carefully pedigreed *Onagra biennis* at various periods of their development, both before and during fertilization. Plants grown from the seeds produced under this influence varied profoundly from their parents. Old characters disappeared, and new ones became evident. The treatment followed by heritable alterations was one in which the pollen grains were exposed for twenty-four hours to rays from radium of 1,500,000 activity, contained in a sealed glass tube. Thus only the X-rays and possibly the more penetrating of the Beta-rays were effective. The three individuals with thick, leathery leaves, which resulted from this treatment of the pollen, have already produced a second generation in which the new characters are seen to be reproduced, and, while awaiting the continuance of this work, it may be assumed with fair certainty that the atypic strain will continue its development parallel to the parental one.

Other striking departures in ontogeny were secured by exposure of the pollen and the ovary before and after fertilization, and also by treatment of maturing seeds, which were not transmissible. Some slight modification of the technique might well secure more extensive results and also permit an analysis of the difference, if any, between somatogenic and oögenic inductions and also illuminate the matter of the appearance of bud-sports.

EFFECT OF SOLUTIONS ON GERM-PLASM

The idea that solutions of various kinds might be introduced into the plant, and that modifications of the ontogenetic procedure might be thus brought about, has been in the minds of many workers in the laboratory. Developing inflorescences have been excised and set in vessels containing salt solutions, and in other cases substances were applied to cut surfaces of the vegetative parts of the reproductive organs without result.

This in part was suggested to Darwin by vegetable galls, and in the first chapter of the *Origin of Species* (page 7) we find him saying:—

> "Such facts as the complex and extraordinary outgrowths which invariably follow from the insertion of a minute drop of poison by a gall-producing insect, show us what singular modification might result in the case of plants from a chemical change in the nature of the sap."

That his interest in this matter was continued is evidenced by the following from *Life and Letters*:—

> "Shortly before his death, my father began to experimentise on the possibility of producing galls artificially. A letter to Sir J. D. Hooker (November 3, 1880) shows the interest he felt in the question:—
>
> "'I was delighted with Paget's Essay.[1] I hear

[1] *Disease in Plants*, by Sir James Paget. *Gardeners' Chronicle*, 1880.

that he has occasionally attended to this subject from his youth. . . . I am very glad he has called attention to galls: this has always seemed to me a profoundly interesting subject; and if I had been younger would take it up.'

"His interest in this subject was connected with his ever-present wish to learn something of the causes of variation. He imagined to himself wonderful galls caused to appear on the ovaries of plants, and by these means he thought it possible that the seed might be influenced, and thus new varieties arise. He made a considerable number of experiments by injecting various reagents into the tissues of leaves, and with some slight indications of success." [1]

In response to a request for a more detailed account of work that may have been done on this subject by the elder Darwin, Professor Francis Darwin writes under date of November 27, 1908:—

"I am sorry that I can give you no further information about the experiments on galls. My recollection is that we tried only injections with leaves and stems, and that no actual experiments were made on ovaries. I have never looked at his notes and do not know where they are at this moment, but I feel pretty sure that no definite results were obtained. I think acetic or formic acid was used in the experiments."

In the course of my extensive cultures dealing with mutations, the theoretical conclusions of De Vries as to the pre-mutation period came up for serious consideration, and in order to obtain some evidence upon this point, as well as to test the assumption that the actual changes upon

[1] *Life and Letters of Charles Darwin,* by F. Darwin, II, p. 517, 1905. New York.

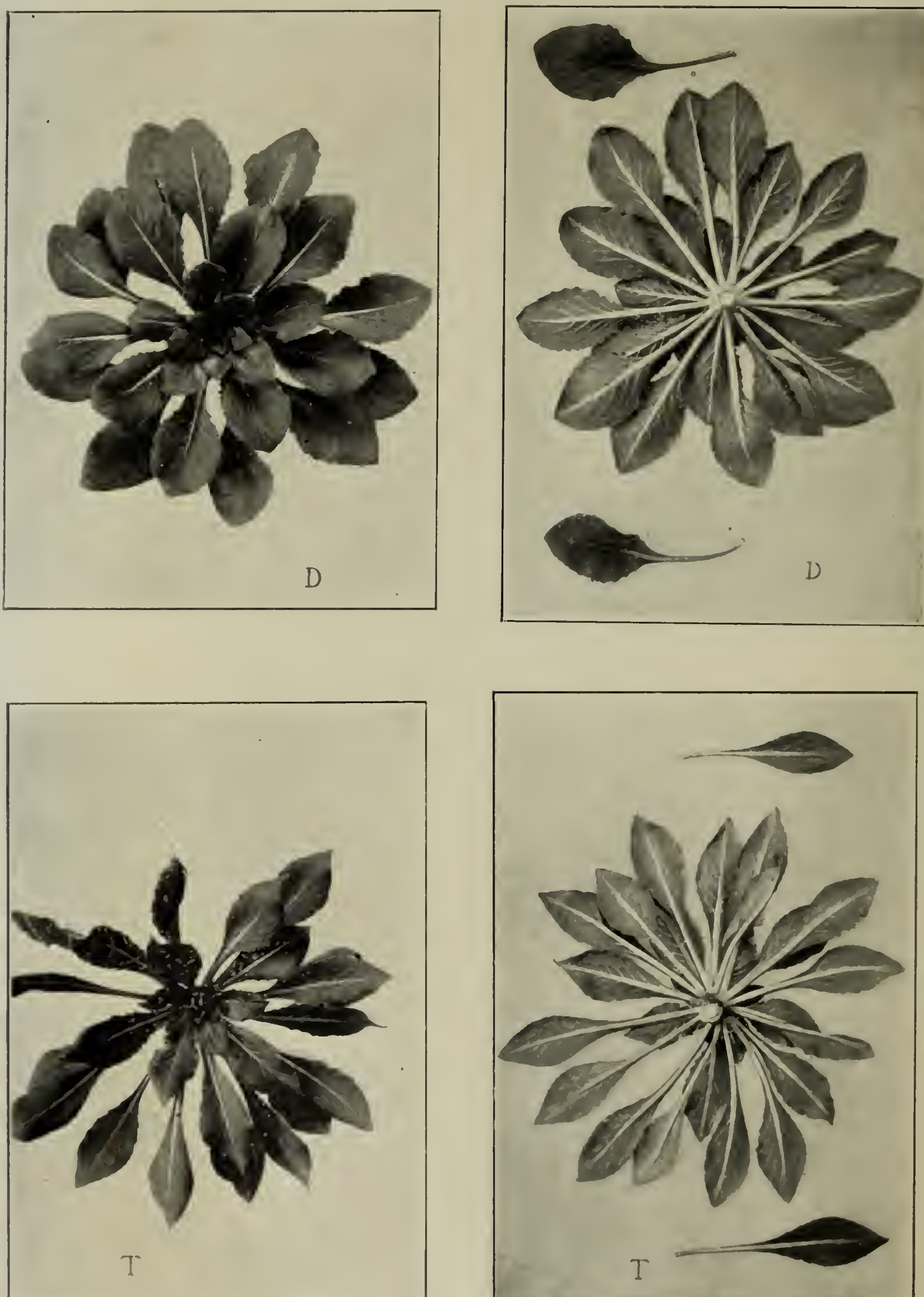


PLATE II.

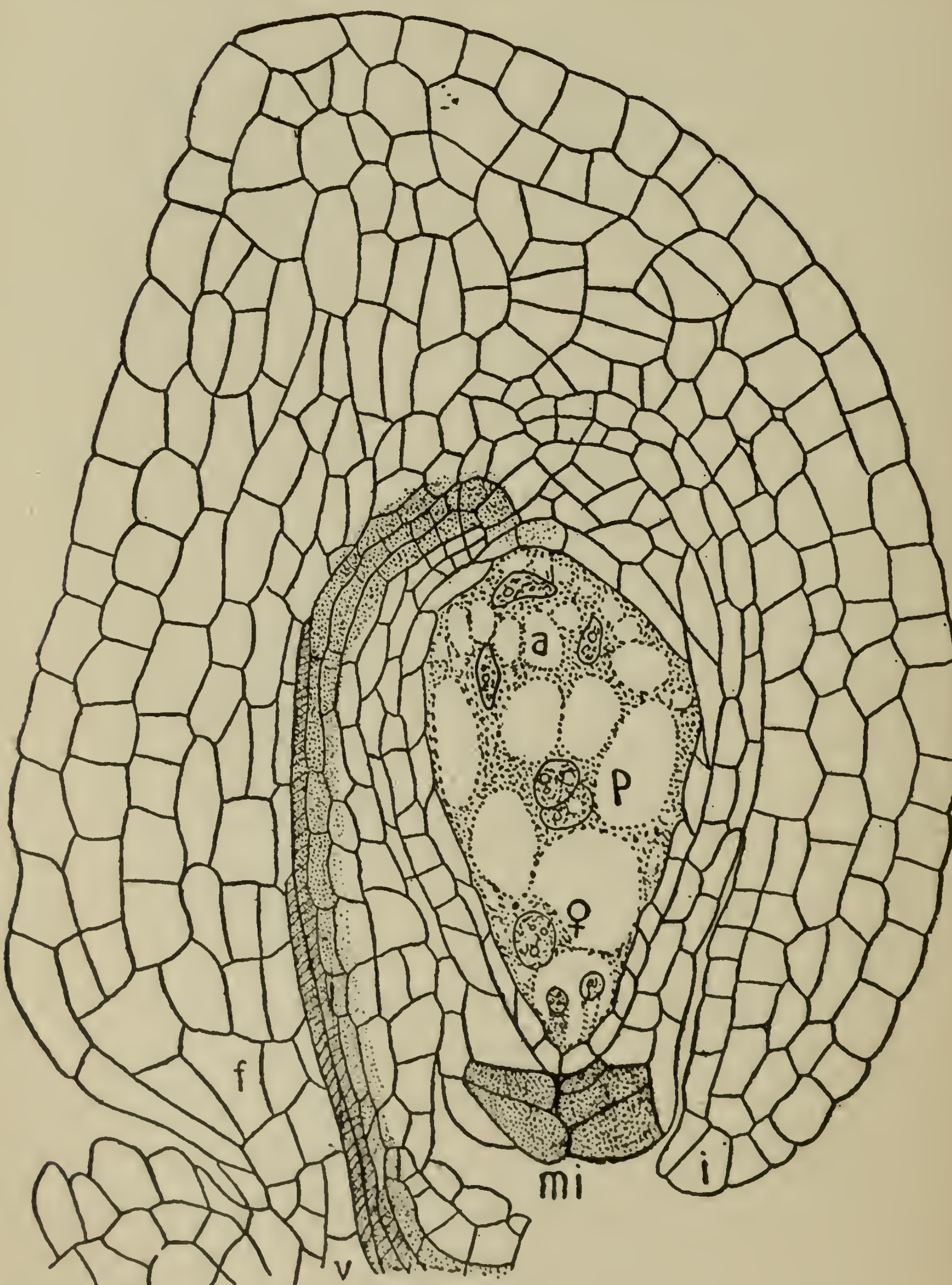
T. T. Upper and lower aspects of rosette of *Œnothera biennis*.
D. D. Rosette of derivative resulting from ovarial treatment with zinc sulphate.

which mutation rests ensue previous to the reduction divisions leading to the formation of the reproductive nuclei, some new methods of experimentation were developed. Among other operations, solutions of sugar, calcium, potassium, and zinc were injected by the use of hypodermic syringes into the developing ovaries of *Raimannia,* one of the evening primroses, early in 1905, with the result that out of the several hundreds of seeds borne by the treated ovaries sixteen individuals were found to be notably atypic, among other characters lacking the trichomes which are so conspicuous with the parental form. These reproduced themselves in the second and third generations, coming true to the newly assumed characters.

The same method was tried with *Oenothera biennis* (Plate II), the common evening primrose of waste lands in eastern United States, with the result that two individuals were found among the seedlings which were different from the parents in a series of characters so distributed through the ontogenetic period that the derivatives [1] could be recognized by the first two leaves, while the cotyledons were still waxing. This form is now being cultivated at the Desert Laboratory in the fifth generation, and is being thrown against the climatic selective factors in the mountain plantations at various altitudes.

[1] The derivatives, lettered D in Plate II, are to be compared with the typical young plants, lettered T.

These two successes had been scored by the use of crude instruments, entire lack of information



Schematic section of ovule showing action of reagent, introduced into ovary. *mi*, micropyle, *P*, egg, *a*, antipodal nuclei, *i*, inner integument. The reagent is taken up by the micropylar cells, and also follows the stream of nutritive material around the inner integument to the neighborhood of the antipodal cells.

as to the mechanical action of the reagents, and with plants offering an ovarial structure most difficult to deal with. In the development of the method, non-corrosive syringes of glass with gold needles and an extended list of substances were employed, while a selection of species was made in which the reagents could be brought into contact with the egg apparatus with proportionately least damage to its somatic structures. The substitution of dyes for the substances to be used was found useful in making out the mechanical results of an injection. Since these operations inevitably resulted in the destruction of a large number of ovules, it was found most convenient to work with forms which are characterized by many-seeded ovaries. By this development of technique, more important results capable of definite analysis were secured and a fair basis for a theoretical explanation gained.

Many progenies representing genera in widely separated families are now under observation, but announcement of results beyond those of a year ago will be confined to *Penstemon.*

Penstemon wrightii is a species well marked and readily separable from its nearest relatives, which alone of the genus inhabits the slopes around the Desert Laboratory. It is, therefore, growing under perfectly undisturbed conditions. Various injections of zinc, calcium, and iodine into the young ovaries were made when these structures were not more than 3 mm. long and

two-thirds of that diameter. A large number of the ovaries were killed by this treatment, but many matured. The percentage of germination in the species has been found to be low, however, and of the few hundreds of seeds sown, not more than a fifth germinated, and a few were killed by drought. Eighty individuals grew to make mature rosettes during 1908. Sixty of these progressed so far as to bloom during the season, and of these, twenty offered such material departures from the parental form as to be readily distinguishable by visitors who had not critically examined any member of the genus, or, indeed, had but little knowledge of plants. These twenty derivatives showed eight distinct types, one of which was represented by five individuals, one by four, two by three, one by two, and three by one. One type resulted from treatments with iodine, calcium, and zinc; four types came from a treatment of two reagents, two from iodine alone, and two from calcium alone. The revolution of the corolla segments, the absence of the stiff clump of trichomes from the lower lip, increase in viscidity, mottling of the flower, and adhesion of leaf bases resulting in perfoliation, are some of the distinguishing marks of the new forms. Of these characters some are already displayed by other members of the genus, while some of the progressive and retrogressive changes seem to be taken before any relative had moved in the same direction.

Briefly summarizing the results of the investigations cited it may be taken as safely established that *individually* acquired or induced characters or modifications of existing qualities may be transmitted from one generation to another practically unchanged. The assumption that organisms may make direct fitting or adaptive responses of the soma to environmental factors, which may be impressed on the germ-plasm and transmitted to successive generations, has not been confirmed by actual observation or experimental tests.

This tentative conclusion that somatogenic characters are not transmitted is one with which the following facts must always be taken into account: *A*—the physiological mechanism of organisms, particularly of the seed-plants, is one which offers direct means of communication between the soma and the germ-plasm in the form of reproductive elements, and which might permit the making of enduring impressions on embryonic tissues during ontogeny, or their effective communication to the egg, or sperm; *B*—the experimental and cultural test of the effect of repetition of the action of external agencies upon the soma in inducing hereditary alteration has not yet been seriously attempted, and may indeed include the crucial requisite of the whole matter; *C*—a great number of structures and functions sustain the closest adaptive relation to environic forces, and important correlations

are found among or between organs in a manner difficult of explanation upon any ground except that of simultaneous somatogenic induction.

MECHANISM OF THE INHERITED CHANGE

The modification of heredity brought about by the direct action of various agencies upon the germ-plasm is now safely established, and the available results are sufficient to justify some few generalizations as to the mechanism of the change. The most important evidence as to the nature of the disturbances which may ensue in reproductive elements comes from the work of Gager, who found that the action of radium might eliminate definite chromatin elements during the mitoses of the egg and pollen, and, furthermore, that some of the eggs fertilized by pollen subjected to such irradiation produced a progeny in which qualities different from those of the parental strain were exhibited. It is not proven, of course, that the atypic strain was derived from a fertilization into which one less or one more chromosome entered, and possible disturbances of the autolytic action of the cell might well be as important as the departures from normal mitotic procedure. The well-known influence of temperatures upon these processes and also the readiness with which unusual substances might be thrown into the cytoplasm in the ordinary course of nutrition, suggests that the plant

would be susceptible to modification in the stage between the reduction divisions and fertilization.

This conclusion is borne out by my own results in which solutions were introduced into the ovary during this stage. The extent of the treatments, together with the diversity of results, makes possible an analysis of other features. Thus the induction of more than one form by the use of a single reagent suggests either that different chromatin elements were affected in the separate ovular reactions, or that unlike parts of the chains of catalytic action were interrupted or disturbed by the introduced substances. Some of the compounds used are inimical to enzymatic action, or may be capable of a negatively catalytic effect, or might indeed set up unusual splitting processes, a state of affairs distinctly favorable to the last named alternative.

Not only may irradiation and the introduction of unusual substances occur naturally to the modification of heredity in plants, but the climatic factors may, as in Tower's experiments, exercise an influence upon the reaction velocities of various parts of the metabolic series, or by variations in humidity, regulate the excretion or retention of active substances. All of these possibilities must be taken into account in attempts at explanation of bud-sports or bud-mutations in plants. It is to be seen that either egg or sperm may be affected by experimental agencies, and that the results do not differ in quality or degree. Gager's

atypic forms were obtained by the treatment of pollen; my own from ovarial injections which might have acted upon the egg, or sperm, and Tower's work was with both.

The new forms of beetles and plants which have thus been called into existence sustain the following general relations to their environment and to the strains from which they were derived:

1. Some of the species dealt with were growing in the open, and domesticated forms were not included in the experiments.

2. The newly arisen or modified characters maintained their distinctive appearance when crossed with the parental strains; in some no reversions have yet been shown.

3. Discontinuous departures induced by ovarial treatments in plants were full and constant within the limits of fluctuability with the first generation. Similar abruptness of divergence is exhibited by beetles in some cases, while in others more than one generation, after removal from experimental conditions, was necessary to secure full expression.

4. Many aberrations induced by irradiation in plants and by climatic effects in beetles were of the nature of closely continuous variations, the range of which was widened by the exciting agent. Some of the derivatives of *Penstemon* may prove to be of this character. The single derivative of *Oenothera biennis* obtained by ova-

rial treatment with zinc sulphate is distinctly discontinuous with the parent.

5. Some of the modifications may be regarded as an increase of capacities already present; some imply the loss of characters or structures, and some are acquisitions; in more than one instance qualities new to the genus have been taken on. Changes such as the mottling of a solidly colored flower may be regarded as a loss of a portion of a design, the total effect of which was a shaded or a self color, or it may be taken as a differentiation in advance.

6. The behavior of the newly derived forms when subjected to natural conditions, competition, and possibility of hybridization with parental forms, has been extremely diverse. Some of the beetles have been swamped by hybridization with the parental form; others have displayed some power of endurance. The plant derivatives induced by ovarial treatments were weaker than the parent in some localities, and more enduring in others. The derivative of *Oenothera biennis* induced by a zinc sulphate ovarial treatment is less adapted to xerophytic conditions than the parent, does not readily hybridize with it when grown in contact, and its earlier characters appear to be dominant when crosses are made artificially.

7. The departures obtained by the experimental manipulation of external exciting agencies bear a general similarity to the initiatory

and modificational phenomena exhibited by organisms in a state of nature, and it seems justifiable to conclude that the processes disturbed or set in motion are identical with some of those concerned in the main evolutionary development of organisms.

THE BEHAVIOR OF UNIT CHARACTERS IN HEREDITY

BY

W. E. CASTLE

No one recognizes more frankly and joyously than would Darwin, were he here to-day, the great advance which has been made in our knowledge of heredity since his time. His work and writings have pointed the way to that advance, and it is largely owing to a return to the experimental method of testing hypotheses, which Darwin used so successfully, that the remarkable progress of the last decade has been made possible. We do, therefore, the greatest honor to Darwin if we pause to consider what superstructure of knowledge has been built on the foundations which he laid. This superstructure is, indeed, still in the building, and it is not easy in all cases to distinguish between the solid structure of proved fact and the scaffolding of hypothesis. Still, the attempt should be made, and it will give us encouragement to discover that, notwithstanding the considerable amount of rubbish lying about, there is, nevertheless, good constructive work going on here which gives promise of permanency.

The particular topic which I have been asked to discuss is the behavior of unit characters in heredity.

The subject of heredity units is one to which Darwin gave much thought. With characteristic thoroughness and patience he assembled the facts of inheritance, reversion, bud variation, regeneration, and related subjects, which in his opinion had a common underlying cause, and with deliberation framed a tentative hypothesis to explain them. This hypothesis, which he called pangenesis, was itself short-lived, but has left a numerous progeny. The most important are the idioplasm theories of Weismann and Nägeli, and the theory of intracellular pangenesis of De Vries. Darwin's hypothesis was useful because it set people to thinking, observing, and experimenting. The theories of Weismann, Nägeli, and De Vries were attempts to bring Darwin's fundamental idea into harmony with facts subsequently discovered. All these theories were scaffolding, not masonry.

MENDEL'S LAW

A conception of unit characters fundamentally different from Darwin's, one which antedates slightly the pangenesis theory, but which suffered total eclipse by it, is to-day known as Mendel's law. It accords so fully with a variety of biological facts discovered

since Darwin's time, that we are coming to regard it as the cornerstone of our knowledge of heredity.

The romantic story of Gregor Mendel is known to you, how toiling long years in obscurity hybridizing garden-peas, he made a great discovery only to see it scarce noticed and soon forgotten. He himself, meanwhile, called to administer the affairs of an ecclesiastical establishment, was forced to relinquish his favorite pursuit of scientific investigation, and was thus unable to follow up his great discovery and force it upon the attention of scientists. So he died unhonored by his fellow-scientists and all but unknown to them.

The story of how, a generation later, Mendel's law was rediscovered thrice over is scarcely less romantic. That the rediscoverers, having first established the law independently and then having discovered Mendel, should assign the honor unreservedly to the obscure and forgotten Abbot of Brünn, is a circumstance which should cause us long to remember and honor the names of De Vries, Correns, and Tschermak.

According to Darwin's pangenesis theory, the reproductive cell is made up of minute units derived from and representing each part or organ of the entire body. A few critical experiments instituted by Galton showed this theory to be untenable, and they seem to have involved in public esteem an adverse decision against all less

well-known theories in which the existence of units in heredity was assumed. Such was the fate deservedly of the highly speculative theories of Nägeli, and undeservedly of the generalization reached by Gregor Mendel, a scientific protégé of Nägeli.

Mendel did not frame any complete theory of heredity, but observed, as the result of experiment, that certain characters of plants are, in crosses, inherited by definite proportions of the offspring. He framed in general terms a statement of what those proportions are and advanced a simple hypothesis to account for them. Mendel's generalization we know to-day as Mendel's law, and his hypothesis as the theory of unit characters.

By a unit character in the sense of Mendel's law, we mean any quality or part of an organism, or assemblage of qualities or parts, which can be shown to be transmitted in heredity as a whole and independently of other qualities or parts. Thus Mendel found that the starchy character of the seed of some varieties of garden-peas, which makes the seeds round and smooth when dried, is a quality which may by suitable crosses be replaced by a sugary character, causing wrinkling of the seed on drying. This change of the seed character through crossing may be brought about without essential modification of the other parts of the plant. Round and wrinkled seed forms in peas, Mendel accordingly con-

sidered to be alternative and interchangeable unit characters.

Similarly yellow color of the cotyledons in the seed of peas was found to be a unit character alternative with green color. In animals we find similar simple unit characters to exist. Thus in mammals black pigmentation is due to the presence of a unit character which may be replaced by another changing the pigmentation to brown. Among horned ruminants, such as cattle and sheep, development of the horns depends upon the presence of a unit character which may be replaced by (or perhaps become associated with) another, in the presence of which horns fail to develop.

RECENT EXTENSIONS OF THE THEORY OF HEREDITARY UNITS

In cases less simple than these, a unit character may have more than a single manifestation, as where a plant having flowers of a certain color has also a similar but fainter coloration of the stem, or a mammal with black hair-pigment has also black skin-pigment, while one with brown hair-pigment has also brown skin-pigment. In still other cases, two or more independent unit characters must be present together to produce a single visible effect. This fact was unknown to Mendel. Its discovery constitutes one of the most recent and important advances made in our

knowledge of heredity, and merits further consideration.

Mendel conceived of unit characters as existing always in pairs, one of which might be substituted for the other by suitable crosses. We are now coming to realize that this is an inadequate statement of the matter. What is paired is not the unit character alone, but the entire organism. All its characters and parts have their basis in paired structures in the protoplasm of the individual, one member of each pair being derived from the mother of the individual, one from the father. The cytologist has visible evidence of this fact in the doubling of the number of chromosomes at fertilization, and their subsequent reduction when the reproductive cells ripen; the experimental breeder has evidence of this duality equally convincing as regards many hereditary characters, but the evidence is clearest in the case of characters which occasionally are lost. It is only in such cases that we can with certainty identify unit characters. By comparing an individual which has a certain character with another individual which does not have it, we learn how much that character includes, and we can learn this in no other way. Experimental breeding will show whether the character is simple, is really a unit, or is an aggregate of independent units. Thus if we cross a black guinea-pig with one which lacks black—say a brown one—we obtain only black offspring, but

these bred *inter se* produce both black offspring and brown ones, in the proportion three black to one brown. We thus learn that black is a unit character. It was contributed by one parent to the cross, but not by the other, and transmitted by the cross-bred individual to half its offspring, but not to the other half. This is Mendel's explanation of the 3:1 ratio, now familiar to every biologist.

But if we cross the same black parent in the foregoing case, not with a brown individual, but with a white one or with a yellow one, we may obtain not black offspring, but wild-colored "agouti" ones, which bred *inter se* will produce agouti, black, white (or else yellow) young, with perhaps those of other new classes in addition. Such a result as this puzzled Darwin, and would naturally puzzle any one, but in the light of Mendel's law becomes capable of ready explanation. The production of black pigment is a process in which more than one unit character is concerned; the production of a gray coat involves more units still; how many, can in part be determined by a study of the number of classes of individuals occurring in the second generation from the cross, and the numerical proportions in which the individuals occur in these classes. The point may be made clearer by following through a particular case, to which Darwin makes reference.

Primary color-varieties of rabbits	Constitutent factors
Gray	$\begin{array}{ccccccc} & & U & & & & \\ & & \vert & & & & \\ A & — & C & — & B & — & E \\ & & \vert & & & & \\ & & I & & & & \end{array}$
Black	$\begin{array}{ccccc} U & & & & \\ \vert & & & & \\ C & — & B & — & E \\ \vert & & & & \\ I & & & & \end{array}$
Yellow	$\begin{array}{ccccccc} & & U & & & & \\ & & \vert & & & & \\ A & — & C & — & B & — & R \\ & & \vert & & & & \\ & & I & & & & \end{array}$
Sooty	$\begin{array}{ccccc} U & & & & \\ \vert & & & & \\ C & — & B & — & R \\ \vert & & & & \\ I & & & & \end{array}$

If rabbits of various colors are turned loose together in a warren, the population is likely to revert more or less completely to the gray coloration of wild rabbits. The foregoing is in substance the statement of Darwin; and its correctness is fully established.

THE FACTOR HYPOTHESIS IN RABBIT BREEDING

Before going further it may be well to describe the color varieties of rabbits. These are exceed-

ingly numerous, but for our purpose may be reduced to four fundamental color types in addition to the albino or uncolored type. These four are gray, black, yellow, and sooty yellow. The last I shall for simplicity call sooty. Gray is the original or wild type from which the others have been derived. The gray fur contains both black and yellow pigments, but so disposed as to produce a pattern on the individual hair, viz., a dark base and tip and in between them a band of yellow. The lower surfaces of the body also are whitish. In the black variety the hair pattern is wanting, and the black pigment occurs throughout the length of each hair and all over the body. In the yellow variety black pigment is largely wanting throughout the coat, though present in the eye and, in very small quantities, in the hair. The presence of the hair-pattern is nevertheless suggested by whitish under surfaces, as in the gray type. The sooty type closely resembles the yellow, but has colored under surfaces, instead of white ones. Yellow and sooty correspond with gray and black respectively, but with a greatly reduced amount of black pigment in the fur, so that yellow predominates there.

Let us now consider the relation of these four types one to the other. Gray crossed with any other type produces only gray offspring. Black crossed with yellow produces gray, but crossed with sooty produces black. Yellow crossed with sooty produces only yellow. Sooty disappears

in crosses with any other type; it is recessive in the Mendelian sense with reference to all the others.

Darwin explained the reversion of feral rabbits to the gray type on two grounds: (1) "a tendency in all crossed animals to revert to their primordial state," and (2) the action of a more "natural" environment when the animals are free than when they are in captivity. In reality neither of these conjectured reasons has anything to do with the case. Some varieties will under no circumstances give reversion, if crossed with each other; but reversion may be obtained as readily in captivity as anywhere. Reversion is due solely to the bringing together of certain unit characters, whose joint action is necessary to produce the observed result.

In producing the gray coat characteristic of wild rabbits at least eight independent unit characters are involved. Other color varieties of the rabbit have arisen by regressive variation, *i.e.* by loss, more or less complete, of one or more of these unit characters.

To illustrate the matter, let us consider the result of a particular experiment. Black rabbits were crossed with light yellow (cream) ones, and produced wild-colored gray offspring. These bred *inter se* produced young of a variety of colors, but among them grays again predominated. All the first generation grays seemed to breed alike, producing young of various colors,

but not so those of the second generation (F_2). Among these thirty-two different classes may be recognized, that is, thirty-two sorts which, though all looking alike, produce each a different assortment of young. These assortments are:—

1. Gray only.
2. Gray, and black.
3. Gray, and white.
4. Gray, black, and white.
5. Gray, and yellow.
6. Gray, black, yellow, and sooty.
7. Gray, yellow, and white.
8. Gray, black, yellow, sooty, and white.

Eight other varieties produce the same sorts of young as these eight respectively, but in addition produce dilute pigmented ones of the same color types, *i.e.* blue-grays as well as grays, blue as well as black, cream as well as yellow, and pale sooty as well as sooty. Sixteen other varieties produce the same assortments of young as these sixteen, but in addition produce animals spotted with white in each of the several color types.

The facts briefly stated are now before us. We can distinguish among the second generation gray rabbits thirty-two different kinds, all looking alike but all breeding differently. Out of this apparent chaos the Mendelian theory of unit characters brings law and order; no other explanation has been offered which makes anything but chaos out of the situation. The number of distinguishable classes, thirty-two, shows that

five independently variable characters are involved; the proportions in which the several sorts of young are produced by each class of gray parent confirms this conclusion. If the number of independent unit characters concerned were one greater, as it is in guinea-pigs, the total number of classes of parents would be doubled to sixty-four; if it were one less, the number of classes of parents would be reduced one-half, to sixteen.

What now are the five variable unit characters concerned in producing the gray coat of a rabbit and what are their relations one to another? In answering this question it will be necessary to mention a sixth unit character which contributes to the result, though not itself variable. It will be convenient also to designate each separate unit character by a letter or symbol. The six unit characters to which reference has been made are:—

1. C, a general color factor, something necessary to the production of all pigment, wanting only in albinos.
2. B, a factor for black, some substance, which acting upon C, produces black pigment; this is in rabbits an unvarying factor, though in other mammals it is often variable.

The four remaining factors modify the action of one or the other of these two; they are:—

3. A, a pattern-factor governing the distribution of black on the individual hair, so that it converts black into gray, blue into blue-gray, and sooty into yellow.

4. E, a factor governing the extension of black over the body generally; in its most extended distribution, black occurs on all hairs of the body, in its most restricted distribution (R) it scarcely extends beyond the eye, and the skin of the extremities, the hair being practically devoid of black pigment and appearing yellow; that this factor is distinct from B, is shown by the fact that it can, in guinea-pigs, be dissociated from B and become associated with brown pigmentation.

5. U, a factor governing the distribution of C over the body; if C covers the whole body (condition U), the whole body is pigmented; if C covers part of the coat only (condition S), the rest is occupied by spots of white. That this unit is distinct from C is shown by the fact that it is transmissible through animals which lack C, that is, through albinos.

6. I, a factor governing the intensity of the pigmentation. It is a modifier of C, for it affects all pigments alike, yellow and brown as well as black, all of which pigments have their common basis in C; but I is distinct from C, for it is transmissible through albinos, which lack C. When I is present all the pigments are intense; when I is absent, or rather weakened to the condition D, the pigmentation is dilute, as in blue and cream, the dilute conditions of black and yellow respectively.

It is clear from what has just been said that these various factors, though separately variable, are not entirely independent of each other. Some produce no visible effects unless others are present. Thus if C alone is wanting, none of the others is visible. To aid in expressing the interrelationship of the factors I think it useful to imitate the organic chemist and employ diagrams. Thus a diagram might be constructed as follows to express the relations of the six factors

in a reproductive cell transmitting the color characters of a gray rabbit:—

$$\begin{array}{ccccccc} & & U & & & & \\ & & | & & & & \\ A & — & C & — & B & — & E \\ & & | & & & & \\ & & I & & & & \end{array}$$

It is possible that in protoplasm we have organic molecules built up in some such way, and that regressive variations arise by dropping off the constituent parts of the molecule one by one. Certainly it is loss or extreme modification of factors that produces the ordinary color variations. If A drops out, we have a black rabbit instead of a gray; if E is replaced by R, a yellow one is produced; if both these changes occur, a sooty one; if U is replaced by S, we have a spotted gray rabbit; if both U is replaced by S, and A is lost, a spotted black rabbit results; if C is lost, we have an albino, whose breeding capacity varies with the number of other invisible factors which remain.

The list of known color factors is not exhausted by those which I have enumerated. One other, a factor for brown pigmentation, Br, has been revealed in the case of the guinea-pig, the mouse, and the dog, by loss of factor B. Brown pigmentation then everywhere replaces black. This factor bears the same relation as does B to both C and E. Some time doubtless we shall see

brown and cinnamon-gray rabbits produced by the same mutation, loss of factor B, which has produced brown and cinnamon-agouti varieties among mice and guinea-pigs. Again there must be in all rodents a factor Y which, acting in the presence of C, produces yellow pigment, but Y has not unmistakably revealed itself by getting lost. It is always present, if C is, and may represent possibly a step on the road to the production of black and brown. Certainly, however, its distribution on the body of the rabbit is independent of the factor E, though subject to U. In the diagram, therefore, Y and Br will probably fall into the positions shown herewith for the guinea-pig:—

$$
\begin{tikzcd}[arrows=dash]
 & U \arrow[d] & & B \arrow[dr] & \\
A \arrow[r] & C \arrow[r] \arrow[d] & Y \arrow[ur] \arrow[dr] & & E \\
 & I & & Br \arrow[ur] &
\end{tikzcd}
$$

This diagram would express the interrelations of the color factors, as we now understand the matter, in a reproductive cell or gamete transmitting the wild type of coat. But such a gamete might be formed by some sixty-four different kinds of wild-coated individuals. The only differences, however, between these sixty-four kinds of individuals would lie in whether they contained a single or a double dose of each of the factors enumerated. I therefore propose

further to imitate the organic chemist by placing a subscript, $_2$, after each factor doubly represented in the individual, *i.e.* after every factor in which the individual is homozygous, while elsewhere omitting it. We shall thus have a zygotic formula which will look like a chemical formula, and which will serve the same useful purpose of expressing many facts clearly and in small compass.

The zygotic formula of the pure gray rabbit will then be B_2 E_2 A_2 C_2 I_2 U_2; the gray rabbit which also gives black young will be single in A, but otherwise identical in formula with the foregoing, viz., B_2 E_2 A C_2 I_2 U_2, and so on through the list.

The question will naturally suggest itself, how common are unit characters? Are all the qualities and parts of organisms due to them, or only certain kinds of qualities or parts? Such questions can not at present be answered satisfactorily. It may be pointed out, however, that we are already acquainted with a considerable variety of Mendelizing characters. These include in plants both structural and physiological characters of stem, leaf, flower, and seed. In animals, where a less extensive study has as yet been made and where the organization is much more complex, the unit characters thus far identified relate chiefly to superficial characters, pigmentation, hair-structure, and the like. Certain peculiar variations of the skeleton, digital variations,

and the like, have, however, been shown to Mendelize, and further study will undoubtedly reveal the existence of additional unit characters. We should also bear in mind that we have no means of identifying unit characters except as they drop out of existence in certain individuals. Many unit characters are probably of such vital importance to the organism that they cannot be dispensed with, for when they are lost the organism ceases to exist. In such cases the existence of unit characters, however probable, can not be unmistakably demonstrated by any method now known to us. Fragmentary as our present knowledge is, it is doubtful whether any category of organs, quantities, or parts can be mentioned which is not subject to Mendelian inheritance. If we could only discover some means of suppressing particular unit characters, what an instrument for unraveling the mysteries of inheritance would be ours!

Time does not suffice to discuss the mutability or immutability of the unit characters, the possibility of new characters arising *de novo,* and other interesting but disputed questions. These are matters with which the second fifty years after Darwin will have to deal.

MUTATION

BY

CHARLES B. DAVENPORT

Forty-three years after the *Origin of Species* there appeared the first part of a book by the Dutch naturalist, Hugo de Vries, entitled *Die Mutationstheorie.* Many other theories of evolution have been propounded and defended in the last half-century, but hardly any other has commanded such immediate consideration and received such widespread acceptance. The mutation theory must therefore contain certain evident elements of truth. Let us consider its scope and some of the evidence on which it rests.

MUTATION DEFINED

First of all it is necessary to define mutation in De Vries' sense and to show its relation to other evolutionary principles. Mutation in any strain is a change in the unhybridized germ-plasm of that strain which is characterized by the acquisition or loss of one or more unit characters. There has already been presented to you the evidence for unit characters, a conception first clearly elucidated by Darwin. I think it may fairly be said that the mutation theory rests on the doctrine of unit characters and applies

only so far as that doctrine applies. As even the most extreme neo-Darwinian school recognizes such units with their representatives (determinants of Weismann) in the egg, and as in evolution there must be the acquisition or loss of at least some one character, it might be expected that the idea of mutation as defined above would find universal acceptance. But it has not done so. The difference of opinion relates to the *gradient* of the transition by which a new unit character is introduced or an old one disappears. Mutation in De Vries' sense implies the sudden appearance, complete in the first generation, of the new unit character and its germinal representative, the pangene or determinant. Mutation is regarded by many who call themselves Darwinians as an innovation and as opposed to Darwin's fundamental assumptions. For the neo-Darwinian conceives the determinant as gradually changing in evolution and exhibiting in the adult forms of successive generations the same continuous series that an organ shows in its ontogenetic development. The view of neo-Darwinians is well indicated in the following quotation from Weismann[1]:—

"If I mistake not we may say at least so much that all variations are, in ultimate instances, quantitative, and that they depend on the increase or decrease of the vital particles, or their constituents, the molecules. . . . What appears to us a qualitative variation is, in reality, nothing more than a greater or less, a different mingling of the constituents which make up a higher unit, an

[1] *The Evolution Theory,* Vol. II, p. 151.

unequal increase or decrease of these constituents, the lower units. We speak of the simple growth of a cell when its mass increases without any alteration in its composition . . . but the cell changes its *constitution* when this proportion is disturbed, when, for instance, the red pigment granules which were formerly present but scarcely visible increase so that the cell looks red. If there had previously been no red granules present, they might have arisen through the breaking up of certain particles—of protoplasm, for instance,—in the course of metabolism so that, among other substances, red granules of uric acid or some other red stuff were produced. In this case, also, the qualitative change would depend on an increase or decrease of certain simpler molecules and atoms constituting the protoplasm-molecule. Thus, in ultimate instance, all variations depend upon quantitative changes of the constituents of which the varying part is composed."

So far Weismann. With his accustomed thoroughness he has followed the consequences of his stand that quantitative changes alone are sufficient to account for the processes of evolution, although to do so he has been forced to take the position that the loss of certain atoms from a molecule is merely a quantitative change, and that the appearance of a new quality is quantitative because merely of the order of a change from zero to one! Weismann's argument here degenerates to a mere play of words. Just as good an argument could be made to support the assertion that all changes are qualitative—that 96 is qualitatively unlike 97. But if the ideas are both to be retained, then it must be admitted that a loss of atoms from a molecule, the appearance of

a new kind of molecule, the appearance of red pigment where none was, are all qualitative changes. Weismann's admission that red granules may arise *de novo* in consequence of a molecular change in the germ-plasm is an admission that an organism may undergo a qualitative variation, and this is a mutation. Recalling, then, in recapitulation, that every character of an organism has a chemical basis, that a new character implies one or more new kinds of molecules and that molecular change is essentially qualitative and discontinuous, the conclusion seems safe that variations involving new characters are essentially discontinuous, and consequently of the order of mutations.

DARWINIAN VARIATIONS

At this time the Weismannian view and that of the neo-Darwinists in general is of less interest than that of Darwin himself. What was Darwin's attitude on the question whether variations that play a part in evolution are of the qualitative or the quantitative order? The answer seems to be simple; the question did not present itself to him—our formulation of the matter is a comparatively recent product of scientific analysis. Darwin did recognize saltation as opposed to ordinary variability, and remarks: "It is difficult to drawn any distinct line between a variation and a monstrosity." In his *Variation of Animals and Plants under Domestication,* Dar-

win cites cases of characteristics that he believes to have arisen suddenly, such as the blackness of the japanned peacock, jaw appendages of pigs, short upper jaw and hornlessness in cattle, short-leggedness in sheep and dogs, elongated wool in merinos, and downless fruit in peaches. These instances sufficiently indicate Darwin's recognition of saltation, and if he was led to reject it as the usual mode of modification of species, he did so because the doctrine had a crude form and carried with it the connotation of something teratological or pathological. But is there sufficient evidence that, in rejecting saltation, he regarded evolutionary changes in unit characters to proceed always by the fourth place of decimals? On the contrary, his examples of variations are very unlike the raw material of the biometric school. This is a sample of his idea of variation in poultry:—

> " The tarsi are often feathered. The feet in many breeds are furnished with additional toes. Golden spangled Polish fowls are said to have the skin between the toes well developed."

In the short section labeled " Remarkable variations of Goats," Darwin refers to the great ears of goats of the Island of Mauritius, to the various forms of mammæ, to throat appendages, hornlessness, and presence or absence of toe glands. The entire work on *Variation under Domestication* demonstrates that Darwin frequently, if not usually, meant by Variation the

acquisition or loss of unit characters. Darwin's position has been sadly misrepresented by those neo-Darwinians who have insisted that Natural Selection operates *only* upon variations of the quantitative order. In the *Origin of Species,* Darwin was arguing for continuity and natural law, and accepted the principle "natura non facit saltum" as in accord with the new view. Continuity in nature was his great argument against creation. "Why," he asks, "should all the parts and organs of many independent beings, each supposed to have been separately created for its special place in nature, be so invariably linked together by gradated steps?" Fifty years ago, we must remember, it was the battle of continuity against special creation that was being fought and not the gradual as opposed to the sudden appearance of a unit character.

Recognizing, then, that the mutation theory, far from being opposed to Darwin's theory of the origin of species, would have been welcomed by him, we pass with more satisfaction, on the occasion of this celebration, to a detailed consideration of some of the facts of mutation.

MUTATIONS IN NATURE

The classical case of mutation is that of the evening primrose, named after Lamarck, but henceforth to be no less closely linked with the name of his evolutionary successor, De Vries.

Here is a plant of characteristic form and flower which regularly produces a small percentage of offspring of strikingly different forms—sparsely branched instead of profusely, with brittle leaves instead of smooth, of stunted size and small flowers, with strap-shaped or with ovoidal leaves in place of lanceolate. The unit characters that appear in these peculiar progeny of *lamarckiana* do not intergrade with the corresponding characters of the parents, and, on self-fertilization, are reproduced in successive generations.

While the particular kind of mutation exhibited by Lamarck's primrose is rare, it is common to find species in which an organ appears, in different individuals, in a number of distinct forms constituting the so-called "elementary species" —a term that seems justified since, bred to their like, these forms are reproduced in successive generations. Striking examples of this sort have been found in wild violets by Doctor Ezra Brainerd, and in the shepherd's purse by Doctors Lotsy and Shull. Animals have been less carefully scrutinized for elementary species; but we are not without instances. The true bugs and the straight-winged insects often show both long-winged and short-winged forms, without intergrades. Some tiger beetles, of both sexes, appear either in a brown or a blue-green dress. Wheeler has collected over a score of pink katydids discovered in the United States within recent years, and has noted cases of pink forms of green hemip-

tera. The same green species sometimes have a brown form, too. In these cases the new characters of pinkness and of brownness have undoubtedly arisen suddenly and no intergrades are known. Of the common May beetle, I am informed by Professor Forbes, no less than forty-two forms are known from Illinois alone, several of them difficult to distinguish by superficial characters, all of them readily separated by reference to the copulatory structures, which are different in the various species and in the two sexes. "These structures are so constant," writes Professor Forbes, "that one of my assistants who has handled over ten thousand specimens of one species for determination, says that they are all like castings from the same mold." There are features of this case that certainly look like mutation; particularly the large number of species in a small area separated by non-intergrading differences in one variable organ. But, as Professor Forbes suggests, there is one difficulty in the way of seeing how the differences could have arisen by mutation: the copulating organs in each species are mechanically adapted to each other; and this requires that a coincident and coadaptive mutation occur in the two sexes. But this is a true difficulty only so long as we conceive the entire organ to be a single unit character. There is, however, as little reason for so conceiving it as for regarding the human hand as one unit character instead of many units. The evolu-

tion of mutually adapted sex organs may be readily conceived as follows: Let a new species differ from its ancestor by a character *m;* then, in accordance with the familiar fact of sex dimorphism in unit characters this takes in the two sexes the forms m' and m''. If the two sex-forms are incompatible the new species will come to nought; but if not incompatible the two modified sexes may interbreed and be prevented from breeding with the parent species. By the addition of a *series* of new unit characters, *n, o, p,* etc.—each of which must stand the test of compatibility in the two sexes—a complex dimorphic organ may be built up by mutation. It were wearisome to attempt to catalogue the mutant-like variations that have been recorded among insects and other animals. The great work of Bateson, *Materials for the Study of Variation,* is full of instances, and the entomological and conchological journals are full of many more. Everywhere we find, along with the universal quantitative variation, cases of qualitative, discontinuous variation involving entire unit characters; and these new characters are, probably, judging from our experience with domesticated animals, inheritable.

MUTATIONS UNDER DOMESTICATION

When we study a group of domesticated organisms, such as poultry, we find the races distinguished by characters that do not intergrade

and can not be made to intergrade by crossing. An instance will show how these characters behave. When a black fowl is crossed with an albino, of the Silky race, the offspring are black with a trace of red in the males. When the hybrids are mated together they yield albinos, solid blacks, blacks marked with red, and typically colored red-and-black Games. If you keep on crossing together the red-ticked blacks you always get albinos, solid blacks, red-ticked blacks and Games, and nothing else. Such an experience makes clear, better than any argument, the meaning of unit character, discontinuity, and mutation. Further analysis of this case shows that the black fowl has a unit character—melanic super-pigmentation—that has been added to the primitive Game coloration; and the albino lacks a unit character—the pigment forming enzyme—found in the ancestral plumage. Neither of these unit characters blends in the crossing. If now these unit characters of normal plumage color, excessive melanism, and albinism are today non-blending, essentially unalterable characters, it is probable that they have always been so and were so in their origin. But we have direct evidence as to this matter. In discussing the case of the black-shouldered peacock, Darwin concludes: "The case is the most remarkable one ever recorded of the abrupt appearance of a new form." If the black peacock arose suddenly, so probably did the first black Mediterra-

nean fowl, at a time long before records were kept. Again we find that human albinos appear suddenly, complete, and breed true like real species. We have other cases of semi-albinos of which the history is known. The blue-green Australian parakeets were first brought to Europe in 1831. In 1872 an expert records seeing a single yellow specimen, and by 1877 they had become relatively common in Germany, since they breed true, and now they may be found in most bird-stores of our cities. This yellow parakeet has lost the power of forming black pigment, and the new character appeared suddenly and completely. There is every reason for believing that the yellow canary was thus derived from the green canary, the white Java sparrow from the gray form, and the albino fowl from a pigmented ancestor. The sudden origin of color changes is generally admitted by breeders and field naturalists; and many more cases of suddenly appearing characters might be cited, such as hornlessness in cattle, sheep, and goats; taillessness in cats, dogs, and poultry; hairlessness in horses, cows, and dogs; spinelessness and hairlessness in vegetative organs and fruits; fasciation of the stem and pelorism of the leaves and petals of many plants, and extra digits in poultry, swine, horses, and man. These are examples, merely, for since man first began to domesticate plants and animals hundreds of new characters have appeared suddenly and completely and ca-

pable of vigorous transmission. The frequency of such mutations depends on the number of individuals studied.

Now, during the past four years I have bred, handled, and described over ten thousand poultry of known ancestry. Of striking new characters I have observed many, some incompatible with normal existence; others in no way unfitting the individual for continued life. In the egg, unhatched, I have obtained Siamese twins, anteriorly duplex individuals with shortened upper jaw (like that of the niata cattle, pug dogs, and some carp), and chicks with thigh bones absent. There have been reared chicks with toes grown together by a web, without toe-nail or with two toe-nails on one toe; with five toes, six toes, seven toes, or three toes; with one wing lacking or both absent; with two pair of spurs; without oil-gland or tail (though from tailed ancestry); with neck nearly devoid of feathers; with cerebral hernia and a great crest; with feather shaft curved; with barbs twisted and dicotomously branched, or lacking altogether. Of the comb alone I have a score of forms: single, double, triple, quintuple, and walnut, V-shaped, cup-shaped, comprising two horns or four or six, absent posteriorly, absent anteriorly, and absent altogether. All of these conditions have been offered me without the least effort or conscious selection on my part, and each appeared in the first generation as well developed peculiarities,

and in so far as their inheritance was witnessed each refused to blend when mated with a dissimilar form. For example, the pea × single gives a pea comb which in the next generation yields single and pea; cerebral hernia and no hernia give no hernia in the first generation, but hernia again in the second; taillessness may follow the Mendelian formula, polydactylism approaches it, and the color varieties illustrate it strikingly. In a word, while quantitative variations are never absent in poultry, the sudden appearance and disappearance of full-fledged characters is most striking. Mutation as thus defined presents to the breeder as a common phenomenon. But, say the neo-Darwinists, your mutations are of a teratological sort and have nothing to do with species as we find them in nature. In reply I admit, first, that under domestication many mutations are preserved by man that would perish in nature. It is quite likely that mutations occur almost as frequently in nature as under domestication, but the unfavorable new forms are apt to suffer early elimination. There remains, however, a host of characters that are not detrimental to the individual, and such are not necessarily eliminated. They are teratological only in the sense that they are novel to the species, but they are of the same order as many of the specific differentiæ of feral species. Take, for instance, the passerine birds—what are some of their striking qualitative characters? We find crossed bill

(Loxia), crest (cardinal bird and jay), greatly elongated tail (widah bird), bare throat (bell bird), wattle (huia bird of New Zealand), barbless feather shaft (paradise birds), barbs without barbules (emu-wren), twisted feathers (Chirocylla). The plumage may be glossy black, snowy white, or of broken colors. Since such characters have arisen suddenly, by mutation, in poultry it is fair to conclude that they have probably done so in other birds. Of course there are many characters found in wild birds that are not found in poultry, but where we have evidence that many characters have arisen suddenly, discontinuously, it seems probable that many others, of the same general sort, whose origin can not possibly be known have arisen in the same way. The experimental demonstration of the mutative origin of many characters makes probable such an origin for characters beyond the pale of experimentation.

MUTATION VS. SUMMATION OF FLUCTUATIONS

There are many who are quite willing to admit that mutations do occur, but hold that the part they play must always be regarded as relatively less important than the summation of fluctuations. From this view the mutationist can appeal to the results of experiment. Does the breeder actually introduce new characters into the organic world by summating fluctuations? De Vries insists that the improvement that fol-

lows selection nearly or wholly ceases after four or five generations, and if selection be abandoned the race rapidly returns to its primitive condition. Such has been the experience of breeders of maize, sugar beets, and other crops, and of poultrymen who have sought to increase the egg yield of fowl. Permanent improvement, wherever made, has been effected either by hybridization with a wild form possessing the desired character or by preserving a fortunate sport—a "Shakespeare," as Professor Hansen puts it. Such a sport is a new center from which further progress may start. Recognizing the futility of selecting merely those individuals having the old characters best developed, the most advanced breeders (as at Svälof in Sweden), have systematized the search for single mutations in the midst of extensive seed plats. This law of improvement holds for animals likewise. Four years ago I started several series of experiments to create, in poultry, new breeds by quantitative selection. In one of these I sought to re-create a uniform buff bird like the buffs that arose in China two thousand years ago and are the parents of all known uniformly red or buff breeds. A bird with a red-and-black plumage coloration of the Jungle fowl was crossed with a White Leghorn. The hybrids were white with red on the wings and breast. I then planned to breed together the reddest of these birds and the reddest of their descendants until I should have

gained uniformly red birds. The second generation of the hybrids did show more red than the first, but during the last two years no advance has been made. Again, a cock having a high single comb was crossed with a hen having a typical low pea comb; the hybrid offspring had high combs with papillæ placed high up on each side. An effort to establish by quantitative selection a high pea comb has failed. Dr. Castle tells me that his continued attempts to modify color types of rats by quantitative selection have of late been inefficacious, since regression is very strong toward the original types. The evolution of the American trotter is often cited as a clear case of the results of quantitative selection. Yet is it not true that the advances in recent years have been quite as much determined by the evolution of the sulky and certain technical improvements in handling the trotter and training him? The running record, the result of a larger selection, has, I understand, stood quite still for the last twenty years. Thus even race horses form no exception to the rule that selection, within given characters, soon reaches a period, and improvement must wait on the appearance of a new character by mutation.

This conclusion, far from being opposed to Darwin, would doubtless have been cordially accepted by him, as certain passages in his writings indicate.[1] After describing the early improvement of the gooseberry, he says:—

[1] Compare the instance given at p. 48.

"The 'London' gooseberry (which, in 1852, had altogether gained 333 prizes) has, up to the present year of 1875, never reached a greater weight than that attained in 1852. Perhaps the fruit of the gooseberry has now reached the greatest possible weight, unless, in the course of time, some new and distinct variety shall arise."

De Vries could not have put it better.

MUTATION AND NATURAL SELECTION

But, it is objected, the origin of characters by mutation can not account for adaptation as well as quantitative selection; and adaptation is the preëminent fact in nature. There is no good reason for drawing such a contrast. For the theory of mutation is nowhere incompatible with that of Natural Selection; there may just as well be, there just as truly is, a selection among discontinuous variations as among quantitative variations. In the modern classification of variations selection has come to be associated with quantitative variations; but Darwin did not always so associate it, as I have tried to show. Any variation, of any kind or degree, must stand the test of fitness to survive. If it can not meet the test it must be eliminated. In a field I had 300 young fowl, of which twenty per cent were of mixed colors, and eighty per cent were either white or black. Twenty-four of these birds were killed by crows, and all the dead were either white or black excepting one spotted white and buff. The solid colors are mutants; being *con-*

spicuous on the grass they were relatively unfit to survive, and so they were eliminated. Again the elevation of the tail feathers by the hen is essential to successful coupling with the male; but this is impossible in rumpless hens, and they must all be infertile except for an operation. The wingless cock could successfully couple only with bantam hens, as without wings he could not balance himself while treading larger hens. These examples suffice to show how unadaptive mutations tend quickly to be eliminated. On the other hand, the split spur, the extra toe, the varied forms of comb, the frizzled and silky forms of plumage, even the absence of the oil-gland seem, under the conditions of the poultry yard, to offer no important impediment to survival and propagation. We may conclude, consequently, that selection will act on mutations as well as on graduated variations, eliminating the unfit and letting survive favorable mutations or such as are merely neutral. But, granted that the unfit mutations are eliminated, can such a case of close adaptation as is exhibited by the leaf butterflies (Kallima and the rest) result from a series of mutations? Does not the very perfection of the adaptation indicate that the final touches have been of the quantitative order? Not at all. The perfection of the result may be due to a combination of adaptive unit characters. Bateson, who examined thirty-eight individuals from one locality, finds that they fall into four

discontinuous groups with respect to the coloration of the under side of the wings, *a,* "leaf-veinings" absent or nearly so, ground nearly plain; *b,* ground without veins but with prominent black speckled spots; *c,* veins strong, no blotches; *d,* with blotches, with or without veins. Here at least three unit characters appear; dark lines (veins), black speckled spots, and blotches; but one or all may be absent from a given wing. Between presence and absence of the character no intergrades occur except possibly in the case of "nearly absent" veins. There is reason for concluding that even in Kallima new characters arise fully formed, and that these are numerous enough to affect all the detail of the pattern. If the combination of pattern characters is protective, no doubt it will preserve many individuals from elimination.

There is, moreover, still another way in which mutations may become adaptive; and that is by their possessor selecting a habitat that fits its organization. At the risk of encroaching on the subject of adaptation, assigned to another, I may give an illustration. The whole surface of the earth is scattered over with spores and seeds of plants and the resistant eggs and gemmules of various lower animals. Only if conditions are propitious will they hatch or germinate. Some years ago a dam broke at Cold Spring Harbor in February and drained a lake of eighty years' standing. In the Spring a luxurious terrestial

vegetation sprang up on the lake bottom from seeds lying dormant there. One Winter a ditch was dug through a salt marsh, where the only higher plant was a species of marsh grass—Spartina. The black peat cut from the ditch was piled in a ridge by its side so high that it was no longer covered by the tide. In the Spring various roadside weeds sprang up along the ridges, forming striking lines of vegetation running athwart the marsh. In these cases the germs were present, but failed to germinate until conditions suitable to their organization intervened. So, in general, there are abundant means of dissemination, and for almost every character there is a situation for which it is best suited. In that situation the new character will prove itself adapted to its environment.

THE MUTATION THEORY A KEY TO DIFFICULTIES

The notion of mutation, when fully grasped, solves two difficulties which formerly confronted evolutionists. The first difficulty is the swamping effect of intercrossing. If the usual result of crossing a new character with its absence were a blend of the two conditions, then the difficulty would be a real one. But even in wild species any unit character typically fails to blend when crossed with its absence. The unit characters of violets, shepherd's purse, and spots of beetles are experimentally tested instances. The characters

of domesticated organisms behave in the same way, as illustrated by poultry. Unit characters, then, in so far as they refuse to blend, will not be swamped by intercrossing, but will reappear intact in a predictable proportion in successive generations.

The second difficulty which the mutation doctrine solves is discontinuity between species. Species differ in the presence or absence of certain unit characters. These unit characters are typically discontinuous in their origin. Hence it is futile to look for intergrades; as well might one look for intergrades between carbon monoxide and carbon dioxide. Species are discontinuous because specific characters are discontinuous; and specific characters, in so far as they are unit characters, are discontinuous because the molecular changes upon which they depend are discontinuous.

It is rash at the threshold of any new science to accept any one hypothesis to the exclusion of others. The president of our Association has taught us our duty toward multiple hypotheses. As in the newer chemistry transitions between molecules are becoming a recognized possibility, so it can not be denied that some unit characters may arise gradually; or, as a result of repeated crossing, show true blending and intergrading conditions. Many characters are indeed less or more because they have an ontogeny, and the adults stop at different points in the ontogeny,

as seems to be the case with human hair color. In many instances of geographic variation a gradation of climatic conditions causes a gradation in the development of a unit character all the way from invisibility to strong expression. Doubtless many important discoveries are about to be made in the field of graduated characters. But from henceforth we must, I think, start in our studies of unit characters from the standpoint of their normal discontinuity. While we remember the services of De Vries in insisting on the normal discontinuity of unit characters, we shall, in considering the idea of the unit character, recognize more clearly how great is the debt of biological science to the insight of Charles Darwin.

ADAPTATION

BY

CARL H. EIGENMANN

I. DEFINITIONS

THE chief object in the life of any animal is to leave another like it in its place when it dies. To this end we find numerous adjustments and compromises, adaptations in animals or plants, to place them in harmony with the elements of their physical or biological environment, or to coördinate the different parts of the same animal or plant.

We have major adaptations, such as those of birds, mammals, etc., for aërial respiration, and those of fishes for aquatic. We have also minor adaptations for a particular combination of temperature, light, heat, and the other elements of the physical environment. And, finally, we have adaptations fitting the animal to cope with other animals for a mate and a home, to secure food and to avoid being food.

Aside from adaptations an organism consists of vestiges, and frequently of other characters, that are not adaptations.

Vestiges, we know, are the remnants of past adaptations. Specific characters which are not

vestiges and are not now adaptations may also be past adaptations, or possibly they may become such in the future; it is only certain that they now do not particularly fit the species for survival. Some characters, while undoubtedly adaptive, give the impression that they are overdone. The antlers of the deer, the fang of the saber-tooth, the power of continuous growth of the incisors of rodents, are all adaptations that have in some instances proved to be too much of a good thing.

II. QUESTIONS

In the words of Weismann, the most ardent of the Darwinians, "Adaptations arise whenever needed if they are at all possible."

Adaptations have usually been looked upon as adjustments in the organism to its environment. The suggestion has more recently been made that adapted environments and habits are selected by animals adjusted to them.

Is a man healthy and strong because he practises athletics, or is he practising athletics because his strength inclines him to athletic sports? We have all been modified by our environment and by our activities. It is at least suggestive that some of us have never taken to pole-vaulting and should not have made a record if we had. Evidently there is a difference between the questions of the origin of adaptations in the individual and the origin of an adapted fauna.

The latter is a comparatively simple question. No one, for a moment, would claim that the entire fauna of any particular area of land, or river, or ocean arose where it resides,—became adapted in its present habitat. Adapted faunas are only in small part autochthonous; in large part they are made up by selective migration.

III. ORIGIN OF ADAPTED FAUNAS

For a consideration of the origin of adapted faunas I would invite attention to the fresh water and cave fish-faunas.

The major conditions distinguishing fresh waters from the ocean as an environment for fishes are these: (1) The fresh water contains a very much smaller per cent of salts in solution than sea water. (2) It is, with few exceptions, in continuous locomotion in one direction. (3) It contains sediment. Minor characters distinguishing fresh water differ in different localities.

Fresh-water fishes are not a group different from salt-water fishes. Many salt-water fishes can enter fresh water, and we may for present purposes assume that all candidates for fresh-water existence are adapted or readily adaptable to the fresh water. Adaptations to the second and third of the fresh-water conditions imply peculiarities in habit or structure not possessed by all fishes, and these must, in the main, have been acquired by the marine fishes before they could enter and maintain themselves in fresh water.

The downward current and sediment, if the latter is not too abundant, are not obstacles sufficient to keep an adult fish from entering fresh waters. The eggs and young furnish the point of attack. Among oceanic fishes we have many that have pelagic eggs, others that have adhesive eggs, others that have heavy cohesive eggs, others that have filaments for the attachment of eggs, while others harbor their eggs.

Currents would naturally tend to carry pelagic eggs into the ocean, and as far as I know only one fish with pelagic eggs has succeeded in establishing itself in fresh water, and it, the eel, to the present day, descends to the sea to deposit its eggs!

The other types of eggs of marine fishes are all found in fresh waters, and it is certain that in many cases the possession of eggs of one or another of these sorts has enabled the fish to establish itself in fresh water. Thus the major adaptations were acquired by the ancestors of fresh-water fishes before they were eligible to a fresh-water existence. Innumerable minor adaptations to the peculiar combinations of heat, sediment, light, etc., found in each selected locality, have no doubt arisen in such localities.

When a new water area arises, selective migration is the method of origin of the adapted fauna. The vast territory containing our North American lakes and streams north of the southern line of glaciation, the area from the Arctic south to

near the Ohio River, was covered a few thousand years ago with a sheet of ice. It contained no environment suitable for fishes. The entire fauna and flora of this area, including the fish-fauna, are composed of immigrants that moved in as the ice moved out, and selected the places adapted to each species. While a few of them have become modified since their advent into this area, their fundamental and even their minor adaptations were acquired elsewhere than in their present home. Their adaptation is due to the selection of an adapted environment.[1] The entire area is unsuitable as a place for the study of the origin of all but a few minor adaptations.

The check by cold has not been placed on any individual migration or set limits to the adult. *Rhinichthys dulcis* living in glacial waters and warm springs and the many species adapted to the great range of variation in the temperature in any of our temperate lakes show this. The temperature factor determining distribution is set rather by the adaptation of the eggs to warm or cold water. Our trout, salmon, and white fishes breed largely in winter when the temperature is low. The rate of development of their eggs, like that of all cold-water eggs, is slow.

[1] Of the 152 species of fishes of the Great Lake basin, only 26 species and varieties, 17 per cent of the total, are peculiar to the area. Five of these are but varieties of more southern species, and the other 21 more than represent the extent to which the fauna has become adapted in this area, for eight salmonids and eight cottids are cold water species that may have been crowded out of the region to the south of the basin, by the encroaching heat after the passing of the last glacial epoch.

The warm-water species are warm-water species not because their individuals are incapable of entering cold water, for they do, but because their eggs will not develop in anything but water much warmer than that in which the eggs of cold-water species develop. Their eggs are quickly developed, they are adjusted to fluctuations in temperature, and they respond to such fluctuations in temperature by hastening or slowing their rate of development.

The origin and modification of the cave fauna give a concrete example of the change of location resulting from predestined major adaptations and subsequent minor adjustments. Caves, at the present time, are being colonized by immigration of salamanders of the genus Spelerpes and other animals that have become adapted to a cave existence while living in the dark under rocks, bark, and in other similar places. The adaptation to the conditions of cave existence in this case determines the change of location whenever a cave presents itself.

That minor adaptations occur in these after they have become exclusively cave forms is shown by the structure of the permanent cave salamanders of Missouri and Texas. These have, in large measure, lost their color, and have degenerate eyes.

Not infrequently where we have extreme adaptations to a particular and a peculiar environment, such as are found in the blind fishes to the

caves, or the ability of ichneumon flies to detect and lay their eggs in deeply hidden grubs, we do not really need to account for the extreme adaptation to the extreme environment. The environment and the adaptation may have developed together, as armor-piercing projectiles and armor have so developed together. An illustration is found in the origin of the cave fishes of Kentucky, and still more of those of Cuba.

The cave fauna of Kentucky, so highly adapted it would be hopelessly lost if removed from its peculiar environment, is the result of selective emigration, immigration, and local adaptation. It has become adjusted with the development of the environment it inhabits. At Horse Cave, Ky., a wide valley extends north and south. Tributary valleys come from the east and west. The hills bordering these valleys are limestone capped with sandstone. The north-and-south valley was formed by the Horse Cave River, which originally flowed over sandstone like that capping the bordering hills. No doubt it had a fauna as varied as that of any surface stream. The stream first cut through the sandstone, then into the limestone, in which it gradually dissolved an underground channel. To-day not a sign can be seen on the surface of the streams that are responsible for the valleys about Horse Cave. At least one of them rushes through lofty chambers one hundred and eighty-five feet beneath the streets of Horse Cave.

With this change in the environment, with the disappearance of Horse Cave River from the surface, its inhabitants were compelled to migrate. They moved in two directions to adapted environments. The shore-fishes, channel-fishes, etc., depending on light to find their food and mates, moved out to the Green River, where their descendants live to the present day. The fishes negatively heliotropic, nocturnal, or stereotropic, moved into the holes dissolved in the bottom of the river, followed its subterranean development, and their descendants live to-day in the stream which now flows entirely below the valley. They are colorless and all but eyeless, and have, no doubt, acquired this exaggerated adaptation to their present abode since their immigration. The major adaptation to the cave existence, the power of finding their food and mates without the use of light, they possessed before the formation of the caves, and it is responsible for their present habitat.

Primarily blind fishes do not have degenerate eyes because they live in caves, but they live in caves because their ancestors were adjusted to do without the use of eyes. The degeneration and disappearance of their eyes form another matter.

Wherever in the past environments arose lacking light, they became, and still are, the gathering place of those not dependent upon light.

The Cuban blind fishes offer another example of the concomitant development of a peculiar

and complex environment and its peculiar fauna. The blind fishes of Cuba are members of a family of marine fishes, but live in fresh water in caves of central and western Cuba. They have undoubtedly arisen with the environment in which they now live. The caves are enlargements of rifts in coral reefs. They can be traced from the hills near Matanzas to the shore of Cuba. One of the cracks is seen in the naked coral beach near the Carboneria at the mouth of Matanzas Bay. Another can be traced a little way inland, but a few feet above sea level. The former must contain salt water—the latter certainly contains fresh water. In places similar to the former the nearest marine relatives of the cave blind fishes are found, with eyes. In the latter cave blind fishes are abundant. Evidently the ancestors of the cave blind fishes have always lived in the crevices in which they now live. When these crevices were below the ocean's surface they contained salt water. As the land arose the salt water was gradually replaced by fresh water, to which the fishes as gradually became adapted. The fishes have literally grown up with the country.

Selective migration, the migration to adapted locations, is the chief factor contributing to the origin of adapted faunas. This factor "*change of location*" is to the origin of adapted faunas what the "change of function" is to the origin of adaptive structures.

IV. ORIGIN OF ADAPTATIONS

A. The Problem. The question of the origin of the adaptations themselves is much more difficult. If comparatively few or no new adaptations have arisen in any one neighborhood, nevertheless all these modifications must have arisen somewhere and should be accounted for. Many explanations have been offered. The supporters of some of the explanations adhere to them with the fanaticism of religious belief. But it is necessary to have been reared in the faith to see all that is claimed for them.

Hereditary succession may follow a horizontal line or one that swerves up or down. In other words, successive generations may be alike, in which case the species remain *in statu quo,* or subsequent generations may deviate from their parents in one or more points.

All deviations from the horizontal must start in the germ, or must become located in the germ. The question of the origin of adaptive deviations is the question of how and why adaptive germinal modifications arise, or how adaptive somatic modifications are transferred to the germ. In either case it is the question of how the straight line of exact hereditary repetition may be caused to swerve in a definite direction to reach an adaptive point. This is *the* question of the present generation, perhaps of the entire twentieth century.

PLATE III.

A FEW OF THE NUMEROUS TYPES OF TEETH IN THE CHARACINS.

(From photographs by the author.)

1. Raphiodon vulpinus Spix.
2. Astyanax bimaculatus brevoortii Gill.
3. Serrasalmo humeralis Cuv. & Val.
4. Henochilus wheatlandi Garman
5. Acestrorhynchus falcatus Bloch.
6. Hoplerythrinus unitaeniatus Spix. (Head resembles that of Amia.)
7. Leporinus conirostris Steindachner.
8. Prochilodus scrofa Steindachner.
9. Aphiocharax dentatus Eigenmann & Kennedy.

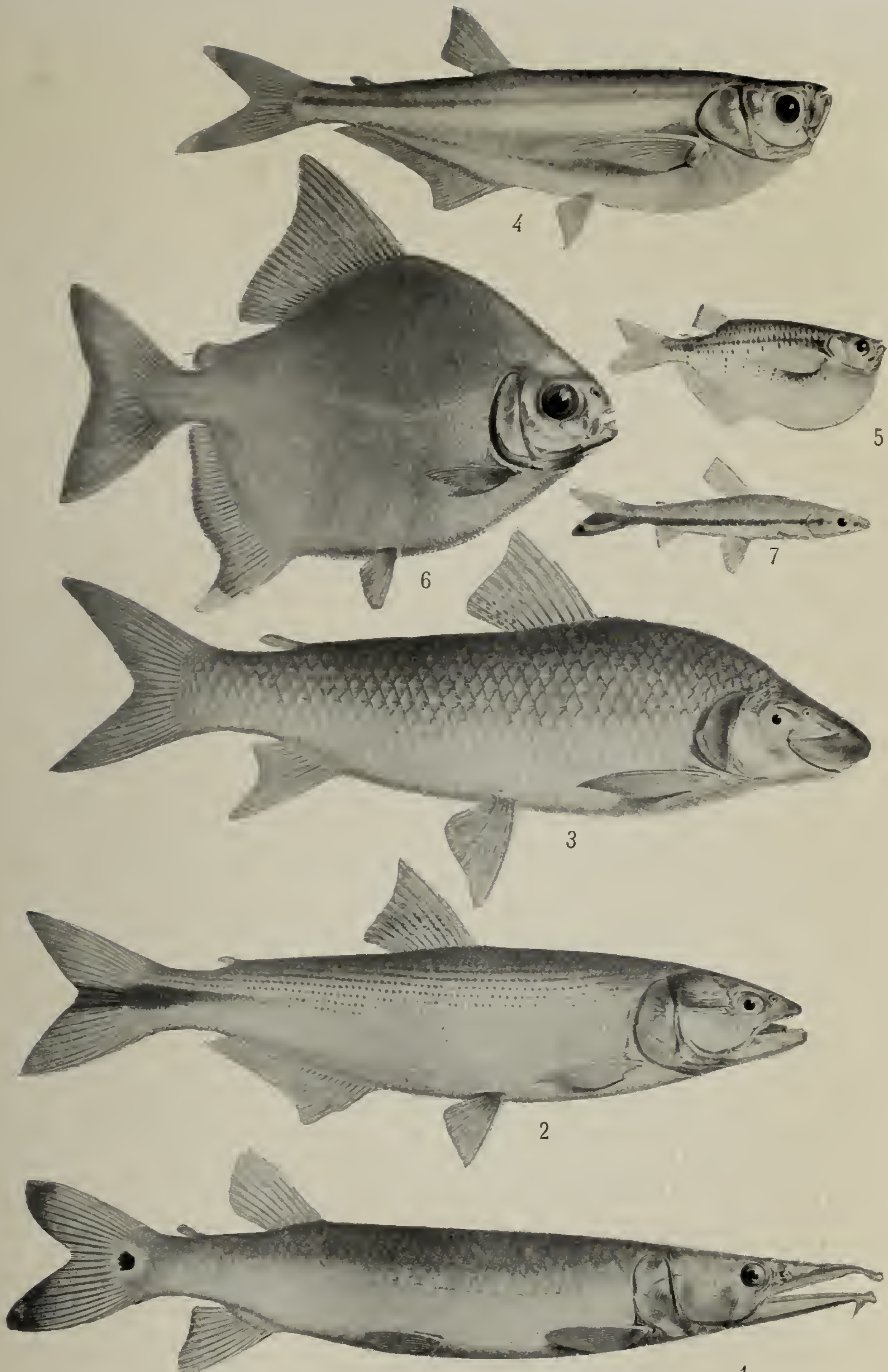


PLATE IV.

Some Similarities in the Characins.

(All figures after Steindachner.)

1. Luciocharax insculptus, a Garpike-like Characin.
2. Salminus affinis, a Salmon-like Characin.
3. Prochilodus longirostris, a Sucker-like Characin.
4. Chalcinus magdalenæ, a fresh water Herring-like Characin.
5. Gasteropelecus maculatus, a flying Characin.
6. Myleus knerii, a Pompano-like Characin.
7. Nannostomus unifasciatus, a Cyprinodont-like Characin.

burrow in the sand in the bottom of the river, others fly with wing strokes through the air above the river, and others occupy all possible spaces between. In appearance they parallel our garfish, our pickerel, our top minnows, our pompano, our trout, our minnows, our suckers, our darters, our fresh-water herrings and shad; and besides these there are a variety of shapes and sizes and adaptations not to be found in other fishes. Chief of these is the series ending in a true flying fish, *i.e.* a fish with wing-like pectorals, large muscles to move them, and the ability to propel itself with wing strokes along the surface of the water for forty or more feet, and to continue its flight for five or more feet in the air.

C. Causes of Adaptations. The causes leading to new adaptations may be intrinsic or extrinsic. The theories of Nägeli, Weismann, and, in part, of Darwin and De Vries, are based on intrinsic causes; those of Buffon, Lamarck, Gulick on extrinsic.

D. Orthogenesis. Nägeli, and in a modified form Eimer, Waagen, Osborn, Whitman, and others, have shown that lines of evolution are orthogenic, predetermined in definite directions. According to Nägeli direction is maintained by the make-up of the protoplasm of the individual. According to Weismann direction is given by the process of germinal selection, helped out by personal selection. By Osborn and others it is recognized but not explained.

The Characins offer us the very best imaginable proof, both for orthogenesis and against its universality. The fact that lines of evolution radiate in so many directions in this family is absolutely conclusive proof that there are many possibilities, that evolution to adaptive points may not only take place along one line or parallel lines, but along very many diverging lines. On the other hand, the fact that there are lines with but few breaks leading from the generalized central type to such aberrant forms as the minute sand-burrowing Characins, duplicating our sand darters, or to the death-dealing Serrasalmo, or the flying Gasteropelecus, shows that, a path of adaptive modification once entered upon by these fishes, evolution along that line may take place, even beyond the point of highest advantage. These lines are not parallel and can not therefore have been the result of the inherent make-up of the family.[1] They have in some way been determined and are being followed to the limit.

E. Mutations. The possibility of divergence in many directions has been experimentally demonstrated by De Vries, who, with others, has claimed that the line of adaptive modification is broken, not bent. Waiving the question of whether the difference between the bend and break is one of kind or degree, permit me again

[1] Similar characters like a pair of canines or ctenoid scales have appeared in very diverse genera both in Africa and in South America.

to point out instances of both in the Characins. I do this fully aware of the fact that some of our experimentalists have claimed that evidence in favor of mutation would not be noted by the systematic zoölogist. It is, however, quite certain that evidence for mutation can not be obtained by experiment only. I have several times found evidence in favor of it in the Characins.

In the Tetragonopterinæ there are parallel genera or subgenera, as we care to look at them. One series has a complete lateral line; the other series has pores developed on but a few scales. No doubt one has been derived from the other—not once but several times. One species, *Hemigrammus inconstans,* is evidently mutating. Two of the four specimens known have a complete lateral line, in the others it is quite short.

Among hundreds of specimens of another species with an incomplete lateral line a single mutation has been found with a complete line. *Moenkhausia australe* by mutation is producing, or has produced *Hemigrammus*. In such cases we have, if a bull is permitted, individuals that are specifically alike but generically different.

While we have many undoubted cases of mutation, there are many reasons why we should not jump to the conclusion that all adaptations have so arisen.

One example of continuous variation leading to an adaptive point is found in some localities of Nicaragua. Here the species of *Astyanax*

æneus, elsewhere with two maxillary teeth, is varying in the old-fashioned way towards a form whose entire maxillary is covered with teeth, *i.e.* it is varying to become a *Hemibrycon.* Of thirty-five specimens there are nine with two teeth, two with three teeth, five with four teeth, five with five teeth, five with six teeth, five with seven teeth, three with eight teeth, and one with nine teeth in the maxillary. No doubt there are some who will claim that these are really mutations, not variations, and I am perfectly willing that they should put this balm upon their prejudices.

The nature of the progressive degeneration of the eyes of blind fishes argues also against the universality of the origin of adaptations by mutation. The degeneration of the eyes of such fishes is a continuous process. The eyes of individuals during their lifetime undergo a continuous degenerative modification leading sometimes to the entire elimination of the eye in the old. The retrogressive changes begin in ever earlier stages of the ontogeny. The differences between individuals are so slight as to exclude the possibility of personal selection, without which either mutation or Natural Selection is incapable of producing results.

There is no evidence that mutation has had any more to do with the production of degenerate eyes than special creation, and we can not even imagine how the degenerate eyes might have

arisen by mutation. Their degeneration is due to orthogenesis or to use-transmission.

F. Environmental Adaptation May Be Intrinsic or Extrinsic. *1. Geographical variation or divergence.* The facts of geographical distribution make it certain that adaptations have not arisen through intrinsic causes only.[1] In fact, they make us doubt at times whether intrinsic causes have had anything whatever to do with the origin of adaptations. If all forms were the result of mutation, due to intrinsic causes, there is no reason why a large river such as the Rio San Francisco should not contain all the modifications possible to the genera inhabiting it, for Shull has shown that new forms may arise in a restricted area. But it does not. Of equal sized streams belonging to different sized river systems the one belonging to the larger system harbors a larger number of species of any genus.[2] And other things equal, the wider the distribution of any genus the more species com-

[1] Tower: *Evolution in Chrysomelid Beetles*, p. 314, says: ". . . All evidence showing them (mutants) to be most rigorously exterminated by natural selection. On the other hand, the study of geographical distribution and variation gives the strongest of circumstantial evidences for direct and rapid transformation in response to environmental stimuli as to the result of dispersion . . . according to the method of trial and error, with natural selection acting as the conservator of the race by limiting the variation to a narrow range of possibilities."

[2] Bean Blossom Creek of Monroe County, Indiana, draining an area of about 250 square miles, is known to harbor in two miles of its course 44 species of fishes. The Colorado, draining an area nearly 1,000 times as large, contains but 33 species of fishes. But Bean Blossom is part of the Mississippi basin that far exceeds the Colorado basin in size and harbors at least 200 species. The still larger Amazon basin harbors at least 700 species.

pose it. In nearly all cases where a species is distributed over a wide, discontinuous unit of environment, *i.e.* an area broken up into isolated parts, the parts contain forms that are measurably different from each other.

A most instructive example is furnished by the Characins. *Astyanax fasciatus* is found from Patagonia to Mexico, except at Panama and the Rio Parahyba. It differs in different localities, and in the Rio Parahyba, near Rio de Janeiro, and at Panama the differences have become of specific value. The species is continued in southern Mexico as *Astyanax æneus,* and in northern Mexico as *Astyanax argentatus.* In other words, in those cases where the divergence has gone far enough we call the divergents species, in those cases where they are diverging, varieties. These geographical varieties are species in the making, just as truly as the elementary species of De Vries.[1]

Isolation is not always accompanied by differentiation. Some species of Galaxias in Patagonia and Australia are identical, while those in different parts of Patagonia are different. Geographical isolation must lead to differentiation if the isolation forces the individuals to live in places on the whole different from their original home. A species (*Astyanax fasciatus*) may be all but identical even if isolated in different rivers

[1] The different diverging lines will be fully considered in my monograph on the Characins, now in preparation.

from Mexico to Patagonia, provided it may occupy the same sort of environment in each stream. There is more environmental difference in the different parts of a cross-section of a river in the Amazon region, or in a mile of the length of a small brook, than there is in the pelagic region of streams from Mexico to Patagonia.

2. Geographical convergence. Each river is made up of many different *units of environment.* The pelagic area is but one of these. Muddy bottom, weedy bottom, stagnant water, swiftly flowing water, are other units. Each has its peculiarly adapted fauna. Different members of the same family may belong to different ecological series, and different ecological groups are made up of members of different families. In shallow, swift water over gravel, in a small stream, the adaptations required are a heavy body, strong pectorals and ventrals, on which the fish sits and which are held in readiness for sudden springs. The conditions and adaptations are the same whether the stream be in North America, in Cuba, or in South America. Fishes are adapted to the conditions in each locality, but the adapted faunas in the three areas are not related. In North America, darters, or diminutive perches, are adapted to this niche; in Cuba it is members of the marine Gobies, and in South America members of the versatile Characins and catfishes. Shape and many other things count

for little among fishes. All shapes occur at nearly all times and nearly all places.

Similarly, blind fishes adapted to caves or other dark places have arisen in many places, but are not necessarily related to each other. The blind fishes of Point Loma are Gobies, and have their nearest relatives in neighboring waters. Those of the Mississippi valley belong to the Amblyopsidæ, some of which live in the terranean streams of that valley. The caves of Cuba derived their blind fishes from the cracks of the coral reefs in which caves were formed. In South America their nearest relatives are the nocturnal catfishes of Brazil and the blind fishes of Pennsylvania have their nearest relatives in the nocturnal catfishes of Pennsylvania.

The burrowing lizards of Florida living as earthworms do, look so much like earthworms that the very chickens do not discriminate against them.

3. Geological convergence or parallelism. Geological records of the simultaneous and similar changes in the form in the mass of species of any area during changing physical conditions are not wanting. For instance, Scott says:—

"The steps of modernization, which may be observed in following out the history of many different groups of mammals, are seen to keep curiously parallel, as may be noticed, for example, in the series of skulls figured by Kowalevsky, where we find similar changes occurring in such families as the pigs, deer, antelopes, horses, ele-

phants, etc. Indeed, one may speak with propriety of a Puerco, or Wasatch, or White River type of skull, which will be found exemplified in widely separate orders."

One adaptation has not arisen once but many times.[1] To repeat, "Adaptations arise whenever needed, if they are at all possible."

4. Origin of geographical and geological divergence and convergence. All these facts tend to show that adaptations have arisen as the result of the peculiarity of the environment. How?

It has been demonstrated many times that the individual is modified by his physical environment. It is claimed on the one hand that the deviation is maintained by its transmission to the germ-plasm, and thus the next generation; and, on the other, that the environment, in some cases at least, directly affects the germ-plasm.

There is a third possibility. In some localities the individuals of certain species are very dark, in others they are practically without color. If the latter individuals are examined closely it is found that they are abundantly supplied with chromatophores, and only the needed environmental stimulus is lacking to bring out the strong color. This is not a matter of the simple expansion or contraction of the pigment, which may take place in a few moments, but the develop-

[1] Among characters that have appeared several times independently in the Characins may be mentioned: The incomplete lateral line, the scaled caudal, three series of teeth in the premaxillary, a pair of canines in the lower jaw, ctenoid scales, incisor-like teeth.

ment of an excess of color under the necessary conditions.

It is possible that other nascent intrinsic adaptations are present in different individuals, unnoticed and inconspicuous until the requisite environment causes them to reach the limit of their individual power, that they are environmental adaptations only in appearance. On the other hand, it is certain that in cave animals there is a gradual bleaching with the removal from the light. It is at first purely ontogenic. But no scheme of selection [1] will account for the progressive reduction in the pigment in successive generations. Nevertheless the color becomes less in each generation. And in the final establishment of the bleached condition in hereditary succession even in the light we have an instance of the transmission of an environmental adaptation.

Where environmental adaptation is the result of a struggle with the physical environment, the struggle is entirely independent of the rate of reproduction. The individual must adapt himself to heat and cold whether alone or not. Temperature and other elements of the physical environment affect many individuals at one and the same time. For this reason the physical environment, when it makes its presence felt, operates in a dramatic way. It attacks the mass, sometimes killing thousands of the non-adapted at one stroke. As long as it does not kill all, the kill-

[1] Mutation is ruled out without selection.

ing must be selective and preserve both those ontogenetically and those innately adapted. The attack being on the mass of species and individuals, it tends to preserve those that are alike.[1]

G. Functional Adaptations. The whales living like sharks look like them. Osborn remarks: "If a primate begins to imitate the habits of an ungulate by becoming herbivorous, it also begins to acquire the dental cusps of an ungulate in about the same order as these cusps would arise in an ungulate."

I could paraphrase Osborn's words for the Characins many times. The Characins have taken on the habits of many fishes and have paralleled them while they diverged from each other. A certain habit and habitat in fishes carries with it a certain regulative adaptation. Living as a sand-darter does, carries with it a sand-darter shape. The question that confronts us first is not, why does the sand-darter habit carry with it a certain form, but what caused Characins to adopt the darter habit?

What caused Osborn's primate to begin to imitate the habits of an ungulate? What caused different Characins to begin to eat mud, crustaceans, plants, plankton, and each other?

Overproduction of individuals leading to crowding, the struggle with the biological environment for food (or light in the case of plants),

[1] No more striking example is found than in the old but uniform deciduous habit of plants of the temperate region.

causes all accessible places to become inhabited. Food itself is dependent on other food, and this ultimately on light, heat, depth, nature of bottom, current, and other elements of the physical environment. The habitat once selected, the effect of the changed physical environment will cause the changes already discussed, and the changed biological environment will cause an animal to adopt a changed mode of existence.

It is again possible either that innate characters in certain individuals of a crowded community cause them to migrate in certain directions, or that chance individuals migrate, and that intrinsic or accidental extrinsic causes then start new activities. It is certain that new activities once adopted the result is individual modifications.[1] It has long been claimed and as vigorously denied that these adaptive individual deviations are transmitted.

The factors of both Buffon and Lamarck hinge on the possibility that somatic modifications are transmissible to the reproductive cells. We have not been able to imagine how somatic changes could so influence the reproductive cells that they could, in their turn, produce individuals

[1] We can imagine that this process of overproduction and consequent adoption of different areas may take place in a small basin, but certainly the larger the basin the greater the diversity of conditions, the greater chance of comparative isolation in different sorts of environments, and the greater the number of species.

No small stream long isolated contains many species of a given genus. Notable exceptions are Orestias in Lake Titicaca, and Chirostoma in the Lerma. What applies to the species of a genus applies with equal force to the genera of a family.

possessing in a measure the same characters. Nevertheless, the transmission of individual environmental adaptations has been established.

No cases of the transmission of functional adaptations as unquestionable as those of environmental adaptations are on record.

It has seemed difficult indeed to devise experiments which would prove that the small somatic changes possible during a lifetime are transmitted. We were not sanguine enough to suppose that in one generation modifications could be effected and transmitted that would surpass natural variability, and which could, therefore, be recognized as transmitted characters. I have long been convinced that the progressive degeneration of the eyes of cave vertebrates, coupled with the differential degeneration of different parts, is due and can be due to nothing but the transmission of functional adaptation. I can not altogether regret that this evidence does not seem to have convinced many others.

The *possibility* of the transmission of somatic characters to the reproductive cells has been shown by the transplantation of ovaries in chicks by Guthrie. He found that a black hen containing an ovary transplanted from a white hen, mated with a white male, did not give white chicks exclusively, as the non-transmissibility of somatic characters would require, but that more than half of the chicks were spotted with black. Also that a white hen containing an ovary trans-

planted from a black hen and mated with a black male gave young *all of which were spotted.* These results, if based on rigorously selected material, ought to convince all but a packed jury that somatic characters are *transmissible* to the reproductive cells. If any one knows of defects in Guthrie's material it is incumbent on him to furnish or define material free from all objections on which his experiments may be repeated; for the method promises a final answer to this much debated question.

H. Conclusions. We are forced to the inevitable conclusions that adaptations are not chargeable to one factor, but that sometimes there has been one, sometimes another, and more frequently several factors have coöperated to bring about the adaptations in any one animal.

It is but justice to Darwin to say that he did not pin his faith to the theory of Natural Selection exclusively. Darwinism is broader than neo-Darwinism, whose insufficiency to account for all adaptations becomes daily more apparent.

After fifty years of study of the origin of adaptations a single sentence from Darwin's *Origin of Species* approaches closely to the general conclusions of to-day, and, "lest we forget," it should be emblazoned on the walls of every Biological Laboratory: "These laws, taken in the largest sense, (are) growth, with reproduction; inheritance, which is almost implied by reproduction; variability, from the indirect and

direct action of the external conditions of life, and from use and disuse; a rate of increase so high as to lead to a struggle for life, and as a consequence Natural Selection entailing divergence of characters and the extinction of less improved forms."

I. A Plea for the Naturalist. I can not close this paper without a plea for the naturalist and systematic zoölogist. "Analysis," says Ruskin, "is an abominable business. I am quite sure that people who work out subjects thoroughly are disagreeable wretches. One only feels as one should when one doesn't know much about the matter."

The systematic zoölogist is liable to lose sight of the woods on account of the trees, and follow the example of Jean Paul Richter's Quintus Fixlein, who collected a vast number of typographical errors, assured the public that valuable conclusions could be drawn from them, and left it to some one to draw them.

The imagination is in Biology as elsewhere the guiding spirit. The trouble is our imaginations are sometimes too heavily loaded with statistics and at other times they fly without the balancing kite's tail of facts. The Paleontologists have contributed so much to speculative zoölogy because their imaginations have been kept alive by bridging their numerous gaps and because they have not been hampered by too great a wealth of material.

Whether we amputate eyes and legs to see them regenerate, determine the chromosomic differences between related species, centrifuge eggs, or invent new plants, potato beetles, guinea-pigs, or poultry, match butterflies, count scales, or measure fossils, we are all at work on the problem of problems, " The origin of adaptations."

Experiment is the watchword of the day; but while we are experimenting in our back yards we should not lose sight of the beauty and the importance of the experiments in landscape gardening and zoölogical gardening, that are and have been going on in our front yards that extend from here to Cape Horn.

DARWIN AND PALEONTOLOGY

BY

HENRY FAIRFIELD OSBORN

On March 4, 1860, Charles Darwin wrote[1] to Joseph Leidy of Philadelphia:—

"Your note has pleased me more than you could readily believe; for I have during a long time heard all good judges speak of your paleontological labours in terms of the highest respect. Most paleontologists (with some few good exceptions) entirely despise my work, consequently approbation from you has gratified me much; all the older geologists with the one exception of Lyell, whom I look at as a host in himself, are even more vehement against the modification of species than are even the paleontologists. I have, however, been equally surprised and pleased at finding that several of the younger geologists, who are now doing such good work in our own geological survey go with me and are as strong as I can be on the imperfections of geological record.

"Your sentence that you have some interesting facts 'in support of the doctrine of selection, which I shall

[1] Darwin's letter to Dr. Leidy is under date of March 4, 1860, in reply, as he states, to Leidy's letter of December 10, 1859.

On March 27, 1860, upon the recommendation of Isaac C. Lea and Dr. Joseph Leidy, Darwin was elected a corresponding member of the Philadelphia Academy of Natural Sciences. It is probable that to the Philadelphia Academy belongs the honor of having been the first foreign society to accord this great work official recognition. This recognition was appreciated by Darwin, as is shown by his reference to it in a letter to Sir Charles Lyell, dated May 8, 1860.

The original letter is in the collection of Dr. Joseph Leidy of Philadelphia, nephew of the great anatomist.

report at a favourable opportunity,' has delighted me even more than the rest of your note. I feel convinced that, though as long as I have strength I shall go on working on this subject, the sole way of getting my views partially accepted will be by sound workers showing that they partially accept them. I say 'partially,' for I have never for a moment doubted that, though I can not see my errors, much in my book will be proved erroneous."

Fifty years ago paleontology was an embryonic science so far as natural philosophy is concerned; beyond the grand outlines of change in the world of extinct mammals and reptiles Darwin knew little of its processes or results. In the letter cited above he is encouraged by Leidy's promise of paleontological support for the general doctrine of evolution; he is even more gratified with the passage relating to Selection. In other words, in this characteristically candid letter Darwin appeals for evidence from paleontology in support of evolution; he hopes that sound workers will partially accept his views regarding Selection; he does not for a moment doubt that much of his views regarding Selection will prove to be erroneous.

A year later, April 26, 1861, Darwin writes to L. Davidson, the great authority on brachiopods, asking him to undertake a piece of work which would test the doctrine of evolution.

" . . . in that book [the *Origin*] I have made the remark, which I apprehend will be universally admitted, that *as a whole*, the fauna of any formation is interme-

diate in character between that of the formations above and below. But several really good judges have remarked to me how desirable it would be that this should be exemplified and worked out in some detail and with some single group of beings. Now every one will admit that no one in the world could do this better than you with Brachiopods. The result might turn out very unfavourable to the views which I hold; if so, so much the better for those who are opposed to me. . . . I know it is highly probable that you may not have leisure, or not care for, or dislike the subject, but I trust to your kindness to forgive me for making this suggestion." [1]

I shall show that the sanguine as well as the questioning prophecies of these epistles of 1860 and of 1861 have been fulfilled to the very letter by paleontology; but in order to place the whole matter in its true perspective, and brighten rather than dim the grandeur of Darwin's fame, let me first briefly picture paleontology as it was in 1859 and as Darwin himself knew it even up to the time of his death in 1882.

It is true that modern, or Darwinian, paleontology, as distinguished from the older, or Cuvierian paleontology, dates from a decade after the publication of the *Origin,* or from 1868, when Waagen [2] first exactly and minutely described the *mutations* which occur in a descent or phyletic series of ammonites, and it is true that this epochal work was followed by others; so that the

[1] *Life and Letters,* II, pp. 366, 367.

[2] Waagen, Wilhelm Heinrich: "Die Formenreihe des Ammonites subradiatus," *Benecke's Geognostische Paläontologische Beiträge,* II, 1868, pp. 185-86.

new paleontology of evolution, as distinguished from the old paleontology of special creation, reached vast proportions before Darwin's death. But all this remained a *terra incognita* to Darwin. Absorbed in his observations on living things, in his vast anthropological, psychological, zoölogical, and botanical researches in his revision of the *Origin* and other works, Darwin never found time or opportunity to grasp the meaning of the Darwinian paleontology. He attempted but failed to understand the work of Alpheus Hyatt, which was directly along the lines of that of Waagen, but unfortunately rendered unnecessarily mysterious and difficult to comprehend through the inveterate American love of word-making. If Hyatt's work had been expressed in Darwin's simple language, as it might have been, then Darwin would certainly have grasped the Waagen principle of mutation, and we should have had the benefit of his marvelous insight into its significance. As it was, like Moses, Darwin led his paleontological followers to the Promised Land, but he did not live to enter it; he gave the impulse to search for phyla, or close continuous lines of descent of animals and plants, *but he himself never observed a single phylum.*

This simple fact is of vast importance in our estimate of the weight to be attached to Darwin's opinions. In contrast with Herbert Spencer he was essentially a deductive-inductive worker; that is, he pursued a trial hypothesis

along the strictest lines of observation, he was less interested in how nature might, should, or would work than in how nature *does work*. Of his trial hypotheses that of adaptation through selection of minute favorable variations he candidly tested by all the facts he could bring together; among these, however, were none of the facts observable only in close phyletic series of fossils. This is a fair way to estimate Darwin and to be influenced by him, namely, by his strict inductive methods and in his times, not in advance of his times.

In the last half century thousands of fossil organisms of all kinds have been exactly studied and compared, more or less complete descent series of vertebrates and invertebrates have been garnered, facts and principles entirely unknown to Darwin, and foreign to the logical mind of Huxley as well, have been revealed; in short, the *data of induction as to how nature does work in the origin of certain new characters* have totally changed in paleontology perhaps more than in any other biological field of observation.

Two grand lines of observation have been followed in paleontology quite independently of each other: first, the minute changes in *phyla of invertebrates* observed in fossil shells by Waagen, Hyatt, Hilgendorf, Neumayr, and many others; second, minute changes in *phyla of fossil mammals* observed by Osborn, Scott, Depéret, Matthew, and many others. It is obvious that the

hard shells of molluscs and the enameled teeth and other parts of mammals are entirely independent parts of entirely different organisms, and that if similar laws have been discovered in such widely distinct fields of observation they tend to show that these laws were of force or of wide potency in living organisms in general.

We are, therefore, now enjoying an entirely new vintage of facts and principles. How far can this new wine be put into the old bottles of Darwin's beliefs? What would Darwin himself say if with his incomparable candor and his incomparable power of generalization he were to examine these facts discovered in close phyletic series of vertebrates and invertebrates, and were to test the conclusions which appear to be inductively derived from them?

Thus two great questions arise on this anniversary day in connection with the two words, *Darwin* and *Paleontology:* first, what has Darwin done for paleontology; second, what has paleontology done for Darwin or for the sum and detail of Darwin's teachings?

DARWIN THE SECOND FOUNDER OF PALEONTOLOGY

The former question is readily answered; as Cuvier was the first, so Darwin was the second founder of paleontology. His contributions to the principles of the science were prepared for

by his familiarity through Lyell with the work of the great Frenchmen Buffon, Lamarck, and Cuvier. These principles were stimulated and made his own by his observations during the voyage of the *Beagle,* and his survey of the extinct life of South America. His comments on what he saw exhibit a close observer of nature, the geologist and biologist, the ideal paleontologist except only in the technical field of anatomy. He himself knew few or no lines of descent, but he felt they must be found, and he set the whole world in search for them. These principles of paleontology were given full expression in the *Origin of Species.* There are in that great work innumerable allusions to what may now be called the working method of paleontology, the method which Huxley formulated and expressed in clear terms in 1880. Darwin believed that the breaks in the geological record caused the interruptions in the hypothetical phyla, and his fond confidence that they would be overcome has been more than vindicated. The impulse which he gave to vertebrate paleontology was immediate and unbounded. It found expression especially in the writings of Huxley in England, of Gaudry in France, of Kowalevsky in Russia, of Cope and Marsh in America. These works swept aside the dry fossil lore which had been accumulating since the passing of Cuvier's influence, and breathed the new spirit of search for the principles of fitness, of descent, of survival, and of ex-

tinction. Thus Darwin gave a new birth to paleontology, as to every other branch of biology.

The second question, what has paleontology done for Darwin, calls not for one but for a series of answers. In some ways it has vastly strengthened him as a natural philosopher or as the seeker of natural causes; it affords more convincing proof than any other branch of biology of the truth of Darwin's grandest contribution to our knowledge of the universe, namely, his complete demonstration, which others had attempted and failed to give, of the law of evolution with all its consequences. In this way it has shown him to be quite infallible; in other ways it has undermined his position and shown him quite as fallible as other great men.

It seems therefore that the most important part which a paleontologist can play in this discussion is to state exactly and clearly what paleontology has to say for and against the special hypotheses set forth by Darwin as well as what it has to say that is entirely new since Darwin's time.

SELECTION

Darwin's own hypotheses of the causes of evolution through *Natural Selection* are concentric or in ever narrowing circles; they center around the broad *survival* of the best fitted groups of organisms of all degrees, of orders, families, genera, species, varieties, of the best fitted single

organs, of the best fitted variations in these, and finally come down to the focal point that the causes of adaptation and the origin of species ultimately center around constant variability and the survival or selection of minute variations. From his exhaustive knowledge of Darwin's work Professor Poulton holds that the great philosopher had in mind as the material for Natural Selection *small variations, congenital and inheritable; he knew well that the material included "great and sudden variations," but he did not believe that they were selected. His variations had no power of developing in definite direction. Direction was given by Selection.* That is, it remained for selection to give direction by choosing from all variations those which happened to be in an adaptive direction.

It is obvious that as we pass from the broad to the minute the theoretic demand upon the selection hypothesis becomes more and more intense, but the tendency of our time is to waive aside theoretic considerations and come down to actual observations and facts and see how far they support the Darwinian and other hypotheses, and how far they call for new hypotheses and interpretations.

Thus the question of the hour is to see what parts of this entire hypothetical system of selection within selection, until we reach the minute, are in accord with modern paleontological evidence.

Let us begin with the broad and proceed to the minute.

Selection of entire animals and parts of animals through elimination. Paleontology not only sustains Darwin's broad induction of evolution, but in an equally convincing manner it sustains his broad induction that Natural Selection is and always has been one of the dominant principles of change in the aspect of the living world. Because of the thousands of facts which he marshaled from every branch of natural history in support of this factor he is entitled to be regarded as the founder although not as the originator of the law of the survival of the fittest. In studying the causes of the extinction of the mammals throughout Cenozoic times,[1] I have been struck by the fact that there is hardly an hypothesis of extinction suggested by more recent research which escaped the more or less serious attention of Darwin. My general survey of the economy of extinction in this great class of animals certainly establishes the existence of a very great variety of causes of elimination, some of which are internal, some external in origin, while all operate under the broad principle of selection. I believe I have found fresh proofs of the *continuous operation of selection on all organs,* because some new and brilliant instances in addition to those gathered by Kowalevsky and Marsh

[1] "The Causes of Extinction of Mammalia," *American Naturalist,* Vol. XL, No. 479, December, 1906, pp. 769-95; No. 480, November, 1906, pp. 829-59.

are adduced not only in support of the broad induction that the fittest survive, but also in proof of the more specific principle of Darwin that certain *single organs,* such as certain types of tooth structure, or of foot structure, have been favorable or fatal to their possessors. This is now capable of statistical demonstration and no longer a matter of highly probable inference, as Darwin left it. The most readily comprehended case is that during the Upper Oligocene and Lower Miocene periods, a large number of entirely unrelated quadrupeds possessed a closely similar pattern [1] in their grinding teeth; it was the one character which they possessed in common and certainly was the one character which led them all alike to extinction.

Selection of the larger variations of proportion. When we approach the further application of the selection principle, however, as more novel with Darwin and more intimately associated with his personal views, namely, his doctrine of the selection of larger variations of proportion, as, for example, in the classic case of the elongation of the neck of the giraffe, we are forced to admit that paleontology neither positively sustains nor destroys this working hypothesis, although the evidence which it presents is *rather favorable than unfavorable.*

By exclusion of other hypotheses, paleontol-

[1] I allude to the grinding teeth technically known as bunoselenodont, that is, with a rounded crown (*bunos*) on the inner side of the grinders, and crescentic (*selene*) ridges on the outer side.

ogy may however be said to lend support to this hypothesis. Changes of proportion in long periods of time, that is, in millions of years, play an enormous part in evolution, as seen by the following contrasts in certain well-known structures, among herbivorous quadrupeds:—

Short-toothed and long-toothed=short-lived and long-lived.
Short-toothed and long-toothed=browsers and grazers.
Short-footed and long-footed =short rangers and long rangers.
Short-headed and long-headed =browsers and grazers.
Short-necked and long-necked =near feeders and far feeders.

Among the horses these very changes of proportion in four important organs, the teeth, the feet, the head, and the neck, constitute a very large percentage of the total evolutionary changes, and result finally in certain phyla of horses becoming long-lived animals, capable of traveling long distances, capable of grazing on the harder kinds of food, and capable of reaching food at a considerable distance from the body. This joint action of heredity, ontogeny, environment, and selection of congenital variations of proportion, appears to best explain the transformation of round-headed or brachycephalic into the long-headed or dolichocephalic forms of the horses as well as of other herbivora, in relation to the browsing or grazing habit respectively. The only explanation which has as yet

been offered for such changes of proportion is that of the selection of hereditary quantitative variations.[1]

I am therefore myself inclined to regard long-headedness or short-headedness in the vertebrates generally as well as the similar phenomena of long-footedness (dolichopody) or short-footedness (brachypody) as in many cases caused by the selection of changes of proportion; yet I freely admit that we can not prove or demonstrate this Darwinian hypothesis through paleontology.

One direct paleontological reason may, however, be adduced in favor of the hypothesis of selection of variations of proportion, namely, changes of proportion do not fall under what I call the law of ancestral control of variation. Head proportions or foot proportions, or, in fact, any other change of proportion can not be regarded as controlled by ancestral affinity, because descendants of the same ancestors soon give rise to very different results. For example, a primitive intermediate (or mesaticephalic) form of skull does not at all control the form of skull which may be derived from it; the animal is free, as it were, to evolve into one of many different kinds of head forms. The point is that hereditary predetermination does not appear in the evolution of proportion and of form as I shall show that it does appear in the evolution of cer-

[1] The fact that this throws little light on the origin of dolichocephaly or brachycephaly in the human species appears to throw the selection hypothesis again into doubt.

tain other new characters, except in so far as an evolutionary tendency once established in the direction of brachycephaly or dolichocephaly is apt to be pursued to its very limits or extremes.

Selection of minute variations. Not only is paleontology not positively conclusive on the hypothesis of selection of large variations, it has nothing positive, but rather something negative to say on the still more intimate or focal feature of the Darwinian hypothesis that minute variations *without direction* in certain specific organs are of survival or of elimination value. Certainly appeal must be made to some other branch of biology on this particular problem, if indeed it is ever capable either of verification or of disproof. Through paleontology we can neither say that Darwin was right or wrong, because we meet with certain peculiar barriers or limitations of paleontological observation. Slight changes of geological level may mark long periods of time. The limitations are not solely due to relative rarity of contemporaneous or synchronous material, because among invertebrates vast numbers of synchronous forms are sometimes brought together so that minute variations may be readily measured, but it is quite another matter to prove through paleontology that such variations are selected. It was Waagen's view that it is not the variations but the less conspicuous *mutations* which reappear in the next generation. This question of the selection of minute varia-

tions is probably *par excellence* a field of research for the biometrician and the experimentalist rather than for the paleontologist.

ORIGIN OF NEW CHARACTERS

We now reach a turning point and pass from differences of proportion, of development, and of degeneration, to the origin of new characters.

Origin of new characters not by selection of the fit from the fortuitous. When, however, this focal point of the selection of minute variations is pressed home as an hypothesis of the origin of *all new* adaptive characters, then paleontology ceases to be either neutral, silent, or inconclusive, and gives to Darwinism a most emphatic negative. In all the research since 1869 on the transformations observed in closely successive phyletic series no evidence whatever, to my knowledge, has been brought forward by any paleontologist, either of the vertebrated or invertebrated animals, that the fit originates by selection from the fortuitous.

Lest the statement be made that this is truly the *sanctum sanctorum* of Darwin's theory of adaptation, let me recall the historical fact [1] that fitness for twenty-five centuries had been the stumbling block of those who sought a naturalistic interpretation of nature; that Kant [2] had

[1] Osborn, H. F.: *From the Greeks to Darwin.* An Outline of the Development of the Evolution Idea, Vol. 1 of the Columbia University Biological Series, 8vo, Macmillan, 3rd ed., p. 248.
[2] *Ibid,* p. 100.

wondered if any one could ever give an explanation of the origin of fitness in a blade of grass; that fitness had become the teleological citadel of the supernaturalists. Darwin was believed by many, but not by all, to have solved this problem of the ages. Let me quote the very recent language of our most profound American philosophical thinker, William James[1]:—

> "It is strange, considering how unanimously our ancestors felt the force of this argument [that is, the teleological], to see how little it counts for since the triumph of the Darwinian theory. Darwin opened our minds to the power of chance-happenings to bring forth 'fit' results, if only they have time to add themselves together. He showed the enormous waste of nature in producing results that get destroyed because of their unfitness."

I repeat: paleontology is not silent, but presents a solid array of evidence against what was never more than an ingenious working hypothesis of Darwin; one he fathered and loved, it is true, but which met little favor in the sturdy and logical mind of Huxley, predisposed as he was to Darwinism. It is now no longer a question

[1] James, William: *Pragmatism.* 8vo, Longmans, Green & Co., New York, 1907, pp. 110, 111. Professor William Bateson gives a similar definition. "*Darwin's Solution.* Darwin, without suggesting causes of Variation, points out that since (1) Variations occur—which they are known to do—and since (2) some of the Variations are in the direction of adaptation and others are not—which is a necessity—it will result from the conditions of the Struggle for Existence that those better adapted will *on the whole* persist and the less adapted will on the whole be lost." *Materials for the Study of Variation, Treated with Especial Regard to Discontinuity in the Origin of Species,* 8vo, London, 1894, p. 5.

of logic but of fact. Does paleontology support this focal hypothesis of fortuity or absence of direction in the minute variations leading to adaptation, or does it destroy it?

The answer is in no uncertain sound. While fortifying all the outworks, paleontology undermines the hypothesis of adaptation through the selection of the directed from the variations without direction by *eliminating the occurrence of the variations without direction* in many important organs. Fortuitous variations as material for advance should certainly be found, if anywhere, in closely successive phyletic series; they have not been found. At the same time this evidence does not leave a vacuum, but replaces the law of chance by another law, namely, that as in the domain of inorganic nature, so in the domain of organic nature *fortuity is wanting,* and the fit originates in many hard parts of the body through laws which are in the main similar to growth,—laws the modes of which we see and measure, the causes of which we do not and may never understand, but nevertheless laws and not *fortuities or chance happenings.*

Now let us inquire how it comes that paleontologists, far in advance of other biologists, have reached this profoundly important principle as to the origin of certain new characters.

The paleontologist observes origins. Having already disclaimed certain powers for paleontology as regards evidence on the evolution factors,

and having still others to disclaim, I may now claim for paleontology as its transcendent power that it alone of the biological sciences can produce evidence of the reign of definiteness, of order, of law in the *origin and early history* of certain adaptive characters, because in the hard parts of animals it alone is in with organs before their beginnings and from their beginnings to their finalities. The beginning of new characters is at once the central problem and the most mysterious problem of evolution. In using the word "beginnings" or "origins" we do not imply *causes* but simply appearances in order of time. It is of unique advantage to the paleontologist as an observer of the origin of new characters that concentrating his attention on single characters entirely irrespective of the species question, which is wholly a by-question, he may trace new characters from the period before their origin, through their first adumbrations, through the stages which may be denominated as origins, through their every subsequent change, through their entire history, in fact. In this long-lived sense as an observer the paleontologist is immortal in contrast with those mortal observers, the zoölogists and experimentalists.

Second, in successive series of animals such as horses, rhinoceroses, or the related titanotheres, the paleontologist may observe the behavior of a very large number of characters at the same time and through long periods of time, some rising,

some falling, one structure taking a rounded form, the structure next it taking a crescentic form, every single element evolving independently in some way. The theory of the simultaneous operation of several factors on different groups of characters and on different kinds of group characters could only suggest itself to a paleontologist working on a very complex animal like one of these big quadrupeds in which countless numbers of characters are simultaneously evolving.

Third, the paleontologist has this further unique advantage: he is in a position to judge which *new* characters are important and which are unimportant; he is, therefore, in a peculiarly favored *judicial* position. By contrast neither the zoölogist nor the botanist is in a position to know whether a new character which he believes to be important is going to persist or not. The difficulty under which the zoölogist labors in this lack of judicial discernment is illustrated, for instance, in Bateson's *Materials for the Study of Variation,* in which he attempts to prove the law of discontinuity from a review of a very large assemblage of characters, the greater number of which the paleontologist would recognize at once as wholly unimportant and non-significant. The only way zoölogy and botany could overcome this disadvantage, as regards the origin of new characters, would be through a series of relay observations extended by successive observers

over long periods of time or through a series of lifetimes. The mortality of the zoölogist, the experimentalist, the botanist, is a fatal handicap, for the reason that they are alike too short-lived to observe and measure those changes in the hard parts (if they exist) which are so excessively slow as to be invisible and immeasurable by mortal eye; while the paleontologist alone is in a position to demonstrate the existence and importance of such slow origins. With his short-time vision is not the zoölogist and botanist more prone to fall into the error of "exclusive hypotheses," and conclude that visible, measurable changes, such as saltations, discontinuities, mutations of De Vries are the most important if not the only changes which are going on in organisms? Thus the paleontologist listens serenely to the fanfare of trumpets of exclusive hypotheses; he knows that time and time alone will show whether these will with other fashions fade.

Sudden origins demonstrable by zoölogy and botany, but not by paleontology. As regards the soft parts of animals and even as regards proportions, changes which occur geographically or in *space* can be measured by the zoölogist, but this does not apply to origins. The first point as to origin, namely, the question of rate or speed of origin, finds paleontology at a disadvantage as a sphere of research. The law of sudden or discontinuous principles has repeatedly been demonstrated in zoölogy and in botany. It

reaches the climax in De Vries' work, where mutation is regarded as an exclusive principle, but discontinuity can never be either demonstrated or disproved by paleontology, since this is the most unfavorable of all the biological fields for the recognition of sudden changes of character, through absence of that abundance of synchronous and contemporaneous material for comparison on which alone it is safe to establish the existence of a mutation. Despite this obvious shortcoming of paleontology, it is noteworthy that the saltatory hypothesis has been—illogically I believe—fathered by a series of paleontologists, by St. Hilaire in 1830, by Cope, and more recently by Dollo and Smith Woodward. It should be borne in mind constantly that wherever a new animal suddenly appears or a new character suddenly arises in a fossil horizon, such appearance may be attributable to the non-discovery of the greater or more minute transitional links with older forms or to the sudden migration of a new type provided with a new organ or organs which have gradually evolved elsewhere. Moreover, the doctrine of sudden appearances is directly the reverse of Waagen's law of mutation. The point, however, is that as a sphere of evidence paleontology neither approves nor disproves the law of discontinuity.

Slow origins demonstrable by paleontology, but not by botany or zoölogy. Paleontology, on the other hand, affords the most favored field for

the observation of slow origins of new characters. It is well known that Darwin was a firm advocate of the hypothesis of slow origins; this was, indeed, consistent with his doctrine of evolution by the adding up of favorable fluctuations. The law of gradual appearance or origin of many new characters in definite or determinate directions from the very beginning I regard as the grandest contribution which paleontology has made to evolution. This law of gradual change in the origin and development of single characters, measurable only at long intervals of time, has now come to rest on a vast number of observations; it is the working basis of the science. Vertebrate and invertebrate paleontologists searching independently of each other on wholly different kinds of animals have reached entirely similar opinions.

Mutations of Waagen. The first, I believe, to express from observation the law of gradual change was Waagen in 1868. The *mutations of Waagen*[1] were originally distinguished by him from the often more conspicuous contemporary fluctuations by the fact that, although seen in minute features, they are very constant and can always be recognized again, but only in successive geological levels, that is, at intervals of many geologic years. Such gradations are observed

[1] Waagen, Wilhelm Heinrich: "Die Formenreihe des Ammonites subradiatus," *Benecke's Geognostische Paläontologische Beiträge,* II, 1868, pp. 185-86.

in single characters; they are the *nuances,* or shades of difference, which are the more gradual the more finely we dissect the geologic column; bit by bit the Waagen mutations are added to each other in different single characters until the sum or degree of mutations is reached which no zoölogist would hesitate to assign specific or generic rank. The essence of Waagen's mutation is orthogenesis or variation in determinate directions, as distinguished from the indefinite variation implied in Darwin's theory.[1] This law received the powerful support of our countryman Hyatt, of the Austrian paleontologist Neumayr, and many others.

In 1889 Osborn,[2] in observing the teeth of large numbers of Eocene mammals, chiefly of the smaller monkeys, horses, tapirs, and other forms, first noticed that new elements here also arise definitely and can only be measured after long intervals of time. He first applied (1890) the term "definite variations" [3] to these characters, but many years later, on observing that many such characters were destined to become adaptive, he gave the same elements the name "rectigrada-

[1] Professor Poulton maintains that determinate variation is precisely what Natural Selection would show, namely *direction* through the accumulation of favorable variations.

[2] Osborn, H. F.: "The Paleontological Evidence for the Transmission of Acquired Characters," *British Association Reports,* Newcastle-upon-Tyne meeting, September, 1889. London, 1890.

[3] "Are Acquired Variations Inherited? Opening a Discussion upon the Lamarckian Principle in Evolution." American Society of Naturalists, Boston, December 31, 1890. *American Naturalist,* Vol. XXV, No. 291, March, 1891, pp. 191-216.

tions."[1] It appears probable, but it is not yet demonstrated, that the rectigradations of Osborn are of the same nature as the mutations of Waagen. Scott[2] in 1894 was the first vertebrate paleontologist to call the attention of his co-workers to Waagen's law among the invertebrates. This principle of *rectigradation* in the origin of many new characters in the mammals cuts both ways; it demonstrates the *absence of the chance happenings without direction,* which form the basis of Darwin's hypothesis of the origin of adaptations, and positively shows that certain new adaptive characters appear definitely and assume adaptive direction from their very minutest beginnings.

To sum up, the law of gradual change in certain determinate, definite, and at least in some cases adaptive directions, through very long periods of time, and the absence of chance or non-direction in the origin of a large number of adaptive and other new characters, is the common working principle both in vertebrate and invertebrate paleontology.

It is thus that the characters which the older paleontological observers, such as Owen, Leidy, Cope, and Marsh, designated as specific and even as generic are gradually built up. We thus wit-

[1] "Homoplasy as a Law of Latent or Potential Homology," *American Naturalist,* Vol. XXXVI, April, 1902, pp. 259-71.

[2] Scott, W. B.: "On Variations and Mutations," *American Journal of Science,* Vol. XLVIII, 1894, pp. 355-74.

ness the origin of what naturalists have been designating as species.

In a lower horizon a cusp of one of the teeth, for example, is adumbrated in shadowy form; in a slightly higher horizon it is visible; in a still higher horizon it is fully grown, and all paleontologists have hitherto agreed to honor this final stage by assigning to the animal which bears it a new specific name. In the face of these continuous series of changes revealed by paleontology the species and genera of Linnæus break up into the continuous chain of the "mutations of Waagen," and for such progressive changes Depéret has proposed the term "ascending mutation."

No theoretical conflict between the mutations of Waagen and of De Vries. It will be shown presently that a very considerable number, if not all, of these slow origins are of a kind which arise from internal causes (intrinsic causes, Williams), that is, in heredity. It is evident that if there do exist hereditary predispositions to mutate in definite directions, such predispositions may manifest themselves very gradually, as in the "mutations of Waagen," or under certain circumstances very suddenly, as in the lesser saltations or "mutations of De Vries." Theoretically, at least, there thus ceases to be any inherent conflict between the hypotheses of "continuity" and "discontinuity"; the latter may represent an intensified or accelerated state of the former.

ADAPTATION

Adaptive nature of certain new origins. Darwin's hypothesis of the selection of variations lacking direction is essentially a law of chance. Origins of many kinds and in many places should be observed; the principle of trial and error should be seen in operation; paleontology should be an especially favorable field for such observation. Yet, as noted above, the mutation law of Waagen and the identical or similar rectigradation law of Osborn is essentially a principle of definiteness and determinateness from the beginning.

Definiteness is not necessarily adaptiveness. The novel feature of Osborn's observations in 1889 on the cusps of the teeth appears to consist in the demonstration of this element of adaptiveness;[1] the new element is not merely determinate, but it is leading directly to utility, and will at a later stage be useful. Thus vertebrate paleontology enables us to establish the law that *certain origins are adaptive in direction from the beginning;* namely, the law of rectigradation.

Such origins of new characters are chiefly *numerical;* something is added to the organ or to the organism which did not exist before in vis-

[1] "Certain Principles of Progressively Adaptive Variation Observed in Fossil Series." Biological Section of the British Association for the Advancement of Science, *British Association Reports*, 1894, p. 643 (title); *Nature*, Vol. 50, No. 1296, August, 30, 1894, p. 435.

ible form, such as the beginning of a cusp or of a horn. The origin of horns has always been a famous problem, because horns are eminently in the nature of new characters. In the great quadrupeds known as titanotheres rudiments of horns first arise independently at certain definite parts of the skull; they arise at first alike in both sexes, or asexually; then they become sexual, or chiefly characteristic of males; then they rapidly evolve in the males while being arrested in development in the females; finally they become in some of these animals dominant characters to which all others bend.

The form, the proportion, the modeling, both of the cusps and of the horns, accord with the proportions of the teeth or of the skulls in which they appear; they are thus correlated in form with other organs. The cusps of the grinding teeth of mammals form a peculiarly advantageous field of observation because they do not depend either upon ontogeny or environment for their perfection; they are born complete and perfect, use and environment destroy rather than perfect them. They thus contrast with the bones, muscles, and many other tissues of the body which depend upon ontogeny for their perfection.

Failure of attempted explanation of adaptive origins by transmission of acquired characters. In seeking explanation of this definiteness or adaptiveness of direction in the origin of certain

new parts, it was natural to first have recourse to the doctrine of the transmission of acquired characters, because it is a well-known principle that certain organs are definitely directed or guided along adaptive lines by use. By reference to my papers of 1889 and 1890, it will be seen that it was in seeking an explanation of *direction,* I was led to support the Lamarckian principle. I do not propose to discuss this enormous question here. Cope concentrated his whole energy on trying to demonstrate Lamarckianism from paleontology, but ended in a logical failure, or *non sequitur,* because the explanation will not apply to *all* cases. Here again I believe that experimental zoölogy rather than paleontology is the best field of research, and that the Lamarckian principle should not be finally abandoned until it is tested by a prolonged series of experiments extending over many years. It is well known that Darwin, for the very reason that he thought he saw in it a working explanation of a directing influence on heredity, finally adopted the Lamarckian principle and proposed his hypothesis of pangenesis. This was also the ground of my first conclusion of 1889, yet owing in the first instance to a trenchant criticism by Poulton, I have for the time abandoned this Lamarckian interpretation, since quite apart from the difficulties in the field of heredity, paleontology appears to offer many objections to it. The objections are simply these: that a very large number of

new, definite, orthogenetic characters which could not have been acquired in ontogeny arise at birth, among them the cusps of the teeth. Since the Lamarckian doctrine either fails or need not be invoked to explain these definite adaptive origins in the teeth, and apparently also in the horns, why invoke it for other adaptive phenomena? This does not preclude the constant operation of the *law of organic selection* [1] or the "selection of coincident variations" advocated by Morgan, Baldwin, and myself, which I still regard as a useful supplementary hypothesis to Natural Selection, explaining many of the alleged instances of the inheritance of acquired characters.

Unknown causes of certain adaptive origins. In 1890 I pointed out that, since the Lamarckian principle gave us a working hypothesis of direction in these adaptive origins, in abandoning the Lamarckian principle we would be left without any explanation, and in developing this idea I came to the conclusion in 1895 [2] that we must appeal to the existence of some unknown factor

[1] Osborn H. F.: "A Mode of Evolution Requiring Neither Natural Selection nor the Inheritance of Acquired Characters (Organic Selection)," *Trans. N. Y. Acad. Sci.,* March and April, 1896, pp. 141-48.

See also: "Ontogenic and Phylogenic Variation," *Science,* Vol. IV, 1896, November 27, pp. 786-90; "Organic Selection," *Science,* N. S., Vol. VI, No. 146, October 15, 1897, pp. 583-87; "The Limits of Organic Selection," *American Naturalist,* Vol. XXI, November, 1897, pp. 944-51; "Modification and Variation, and the Limits of Organic Selection: A Joint Discussion with Professor Edward B. Poulton of Oxford University," *Proc. Amer. Assoc. Adv. Science,* Vol. 46, 1897, p. 239.

[2] "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," *Biol. Lect. Marine Biol. Lab.* 1894, Ginn & Co., Boston, 1895.

or factors of evolution. Subsequent research has convinced me that in these phenomena of the internal origin first of certain determinate characters, and second of certain adaptive characters, we are dealing with the unknown if not with the unknowable, although the latter despairing attitude should not be hastily adopted. The immediate causes are internal, that is, they lie in the domain of heredity rather than of ontogeny, environment, or selection; but lest I might be mistaken on this point, I have devoted several years of thought to the development of a *circle of causes,* so to speak, which I have finally formulated [1] in the law called *the four inseparable factors of evolution.* According to this law I regard heredity not as something inseparable, although extraordinarily stable; on the contrary I have recently expressed the relations of heredity to the other factors as follows:—

The life and evolution of organisms continuously center around the processes which we term heredity, ontogeny, environment, and selection; these have been inseparable and interacting from the beginning; a change introduced or initiated through any one of these factors causes a change in all. First, that while inseparable from the others, each process may in cer-

[1] The Four Inseparable Factors of Evolution. Theory of Their Distinct and Combined Action in the Transformation of the Titanotheres, an Extinct Family of Hoofed Animals in the Order Perissodactyla," *Science,* N. S., Vol. XXVII, No. 682, January 24, 1908, pp. 148-50.

tain conditions become an initiative or leading factor; second, that in complex organisms one factor may at the same time be initiative to another group of characters, the inseparable action bringing about a continuously harmonious result.

This *inseparableness* of internal processes (heredity and ontogeny) and external processes (selection and environment) is not surprising when we reflect that it must have existed from the very beginnings of the organic world.

Thus hypothetically the origins of certain new characters in heredity may find expression not spontaneously, or irrespective of conditions, or from self-operating internal mechanical causes, but through some unknown and at present entirely inconceivable relation between heredity (the germ-cells), ontogeny or habit and use (the somatic cells), environment or external conditions, and selection. This does not preclude spontaneous origins.

Prolonged analysis and synthesis of the evolution processes of the various kinds which led to the enunciation of the above law only served to convince me that certain adaptive origins are immediately matters of heredity whatever their initiation may be in the circle of ontogenetic or environmental causes. We have to do with a *potential* of similar mutations or rectigradations independently.

Here we find ourselves expanding a principle which was clearly foreshadowed by Darwin, and

tions and retardations of characters in heredity which remind us of the well understood laws of acceleration and retardation in individual development.

Degrees of kinship also affect to a certain extent, but not absolutely, the time of appearance or the time of origin of new characters as well as the rate of their development. Thus four lines of Eocene quadrupeds (Titanotheres) branched off independently from one stock; in all the branches we observe similar new cusps arising on the premolar grinding teeth, and similar new horn rudiments rising on the forehead above the eyes, both independently evolved. Neither the new cusps nor the new hornlets appear at just the same moment of geological time; some phyla hasten forward these rectigradations, other phyla retard them.

The independence of single characters and multiplicity of origins. The independence of single characters reminds us of the independence of the "unit characters" as known to the students of Mendelism and of De Vries' mutation, yet the single characters we have in mind are not unit characters in the Mendelian sense because they do not mendelize; they appear in every individual. The independence of single characters in the "Waagen mutations" or the "Osborn rectigradations" is shown by the fact that a considerable number of characters evolve in a perfectly regular and lawful succession. Each char-

acter is a law unto itself, yet all subserve the general good. For example, a new horn rudiment arising on a brachycephalic skull will be broad or rounded; if it arises on a dolichocephalic skull it will be elongate or oval. Thus in a large quadruped like a horse, a tapir, a titanothere, or a rhinoceros each horn, each tooth, each bone of the skull and skeleton, and by inference all the hard parts as well as all the soft parts of these animals in each phylum, have two sets of relations:

I. In the origin of new characters each phylum will evolve, *like* other phyla, hypothetically through inherited predispositions. Thus from forty to forty-eight new characters will similarly arise in a number of phyla in the grinding teeth alone.

II. In changes of proportion and in rate of evolution each phylum will evolve *unlike* other phyla, through freedom from hereditary predisposition in matters of form, proportion, and rate of evolution.

These are the conclusions which I have reached after twenty-two years of very precise work on the evolution of the mammals. Besides exactly observing primates, horses, rhinoceroses, during the past seven years I have devoted myself to still more precise monographic work on the group of titanotheres, bringing together great quantities of material, and with the assistance of Mr. W. K. Gregory making thousands of exact ob-

servations and measurements. Thus the evolution of the group has been traced from a small, hornless animal, of the size of a sheep, to a gigantic horned quadruped little inferior to an elephant. I have realized that the origin of all changes which are discovered in the skeleton must be credited to one of the four factors which take part in evolution, namely:—

HEREDITY.
ONTOGENY.
ENVIRONMENT.
SELECTION.

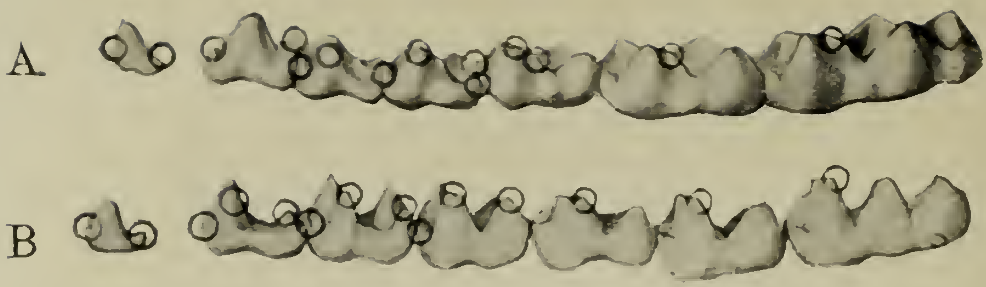
Thus new characters which can not be credited immediately to selection, to ontogeny, to environment, must by exclusion be attributed to heredity, these are the mutations or rectigradations.

METHOD OF EVOLUTION (TITANOTHERÆS)

An interpretation of the evolution of a family. In picturing the evolution of this great famliy of quadrupeds, the titanotheres, through a long period of time and with an unique sequence of material, may we not interpret the facts by imagining a continuous interoperation of the four chief factors, and analyze what we see somewhat as follows?

First, these animals are all of the *titanothere* kinship and of the larger *perissodactyl* kinship. The ordinal kinship and the family consanguinity

PLATE V.

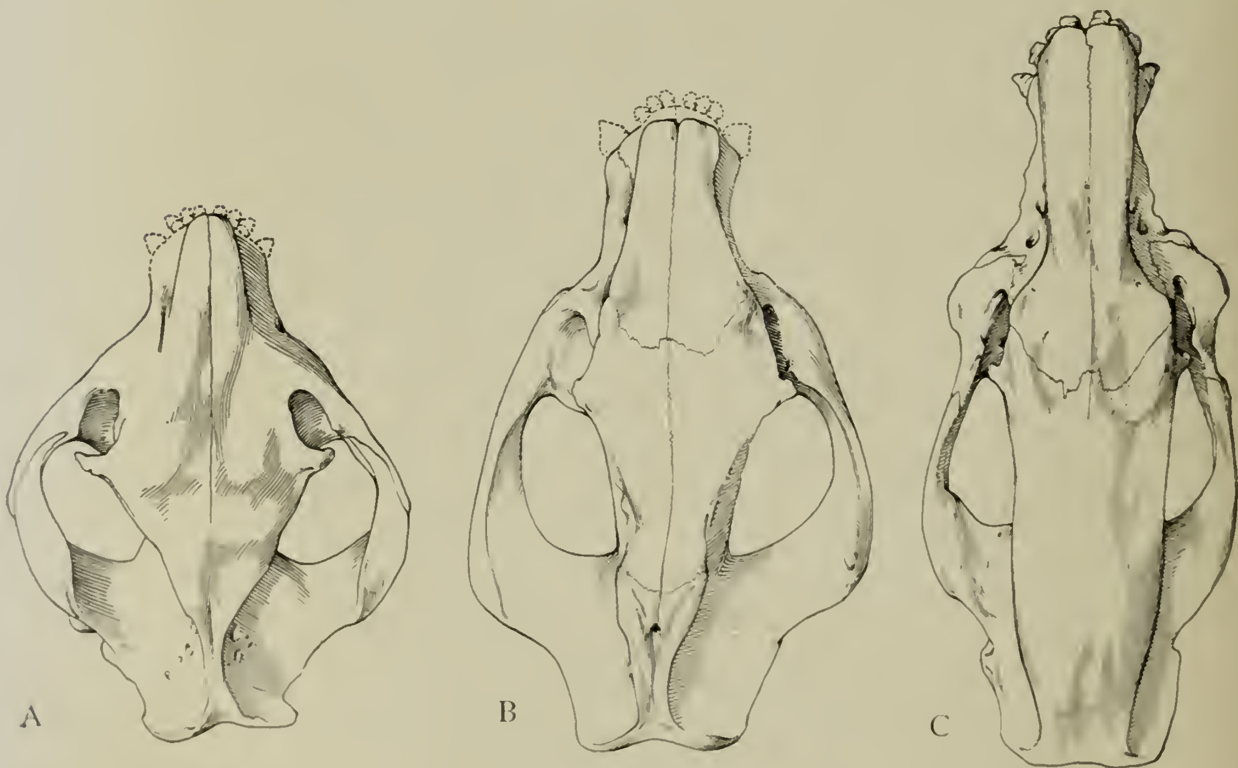


RECTIGRADATIONS IN THE TEETH OF EOCENE UNGULATES.

A. A primitive Equid, *Orohippus* sp.
B. A primitive Titanothere, *Palæosyops paludosus.*

From specimens in the American Museum of Natural History. Internal view of lower teeth.

The circles mark the cusps which appear independently in the different phyla; they are at first barely visible but increase in size in successive geological levels.



TOP VIEW OF THREE SKULLS OF EOCENE TITANOTHERES ILLUSTRATING BRACHYCEPHALY, MESATICEPHALY, AND DOLICHOCEPHALY RESPECTIVELY.

(From specimens in the American Museum of Natural History.)

A. *Palæosyops major*, brachycephalic.
B. *Manteoceras manteoceras*, mesaticephalic.
C. *Dolichorhinus cornutus*, dolichocephalic.

(different from that of the tapirs, rhinoceroses, or horses) apparently tincture and condition many things which happen in the evolution of this group. There are forty-four grinding teeth altogether; twelve of these teeth (the molars) early attain their final form, but are destined through family kinship to lose certain characters and to change their proportions through generic kinship; twelve others (the premolars) have not attained their final form, but gradually do so through the origin of from forty to forty-eight new characters, each of which appears to arise through an unknown law of hereditary predisposition, which operates alike, through ordinal kinship, not only in the titanotheres but in all other odd-toed or perissodactyl mammals to which the titanotheres are related. Changes of proportion in the skull, whether toward breadth (brachycephaly), or toward length (dolichocephaly), affect the form of the grinders as a whole and thus the birth-form of each of these new cusps. The immediate cause of changes of proportion is not interpreted as due to hereditary predisposition, because in teeth, in skull, in foot and limb, and even in horns each generic branch or phylum from the original stem forms of titanotheres acquires its own proportions. Thus changes of proportion are interpreted rather as immediately affected by ontogeny, by the mechanics of use and disuse, by an environment which favors some rather than other proportions, but especially by the selection

of variations in proportion which coincide with the needs of the phylum.[1]

No abrupt variations (mutations) have been observed in the evolution of the titanotheres, but this in no way renders it inconceivable that skeletal mutations in the De Vries sense have produced new races in certain phyla. The addition or loss of a vertebra in the sacral region, which appears to distinguish certain titanothere phyla, may be a case of such sudden inheritable mutations.

Independently in four or five Eocene branches of the titanothere stock the horn rudiments very gradually arise, apparently through hereditary predisposition or family kinship, as rectigradations, at the junction of the nasal and frontal bones. As in the case of the cusps, the shape of these horn rudiments is from the first conditioned by the respective breadth (brachycephaly) or length (dolichocephaly) of the skull.

The branches or sub-phyla become more and more sharply distinguished from each other by increasing brachycephaly or dolichocephaly, brachypody or dolichopody, apparently through congenital variations of proportion accumulated by selection and guided by ontogeny through "organic selection." The animals belonging to

[1] It is important to note, on the authority of Professor Castle, that proportions of the skeleton and probably of the teeth are not inherited as distinct "unit characters." Inheritance of bone size and shape seems to be as a rule regularly blended by interbreeding and without subsequent Mendelian splitting.

these branches appear to have chosen their own local environments, whether in localities favorable to grazing or to browsing, and in turn congenital changes of proportion would be favored by selection if in the right direction. The transformation into brachycephaly and dolichocephaly is brought about through independent changes of proportion in every bone of the skull, as ascertained by exact comparative measurements. A trend once established in either direction seems to constitute a sort of " hereditary momentum " or predisposition, which leads to great extremes of brachycephaly, on the one hand, or dolichocephaly on the other, as shown in the accompanying cut. The rudimentary horns, at first barely noticeable as the faintest convexities of the skull invariably appearing at the junction of the frontals and nasals, and produced by a thickening of the cellular spaces, are first observed of equal size in the males and females; later they become more prominent in the males than in the females; finally they assume vast proportions in the males and present an arrested development in the females. At the summit of the Eocene the extreme dolichocephalic and brachycephalic phyla die out, and in the Oligocene a new series of phyla arise. Among these the long-horned forms appear through selection to develop the horns at the expense of other characters, the males with the longest horns probably securing the most females and becoming the chief breed-

ers. It is especially noteworthy that in these long-horned phyla the main incidence of selection seems to be diverted to the horns from the teeth which appear to be dwarfed or arrested in evolution. In the short-horned phyla, on the other hand, including one series at least, protected by more slender limbs and more rapid movements, the teeth are constantly sharpened and improved; this may be interpreted as caused by the selection of changes of proportion in the teeth.

The teeth, however, of all these phyla of titanotheres are of a mechanical type which does not admit of further evolution; they have reached a stage which is a *cul-de-sac*,[1] beyond which no progress is possible. The change of environment and of flora, therefore, finds these animals incapable of further mechanical betterment either through heredity or through the selection of variations of proportion. All the titanotheres become suddenly extinct, and it is noteworthy that all other herbivorous quadrupeds having this *cul-de-sac* type of grinding tooth also became extinct in North America and in Europe either during the Oligocene or Miocene periods.

This is an outline of the only theoretical interpretation which can be offered at present. In it heredity, ontogeny, environment, and selection are supposed to be in continuous interaction or

[1] Osborn, H. F.: "Rise of the Mammalia in North America." Vice-Presidential Address before the American Association for the Advancement of Science. Section of Zoölogy. Madison, Wis., August 7, 1893.

interplay. One feature has been omitted: that is, that all the branches of all the phyla, with one exception, show a continuous and progressive increase in size. This increase in size is, however, itself interpreted not only as a response to favorable environment, but also to the selection of hereditary variations in size due to the fact that the larger quadrupeds are better able to stand off the attacks of their carnivorous enemies.

CONCLUSION

This interpretation, finally, is seen to include the coöperation of factors recognized by Buffon, by Lamarck, and by Darwin, except as to the transmission of acquired characters, which is left in doubt. There is, however, a new principle in the "mutation of Waagen" or "rectigradations of Osborn," unknown to Darwin and due to causes entirely unknown to us at the present time, and perhaps, as already intimated, unknowable. In this connection it is interesting to recall the comment of Aristotle [1] on the survival-of-the-fittest theory (the bracketed insertions [ ] and italics are our own):—

"What, then, hinders but that the parts in Nature may also thus arise [namely, according to law]. For instance, that the teeth should arise from necessity, the front teeth sharp and adapted to divide food, the grinders broad and adapted to breaking the food into pieces.

[1] Osborn, H. F.: *From the Greeks to Darwin,* 8vo, Macmillan & Co., 1894, p. 55.

" [Another explanation may be offered.] Yet, it may be said, that they were not made for this purpose [*i.e.* for this adaptation], but that this [adaptive] purposive arrangement came about by chance; and the same reasoning is applied to other parts of the body in which existence for some purpose is apparent. And, *it is argued, that where all things happened as if they were made for some purpose, being aptly* [*adaptively*] *united by chance, these were preserved, but such as were not aptly* [*adaptively*] *made, these were lost and still perish,* according to what Empedocles says concerning the bull species with human heads. This, therefore, and similar reasoning, may lead some to doubt on this subject.

" It is, however, impossible that these [adaptive] parts should subsist [arise] in this manner; for these parts, and everything which is produced in Nature, are either always, or, for the most part, thus [*i. e.*, adaptively] produced; and this is not the case with anything which is produced by fortune or chance, even as it does not appear to be fortune or chance that it frequently rains in winter. . . . If these things appear to be either by chance, or to be for some purpose, and we have shown that they can not be by chance, then it follows that they must be for some purpose. There is, therefore, a purpose in things which are produced by, and exist from, Nature."

Paleontology at present seems to support the philosophical contention of Aristotle, that when we come to the minute slowly progressing internal changes, the fittest originates in law.

EVOLUTION AND PSYCHOLOGY

BY

G. STANLEY HALL

DARWIN'S CONTRIBUTION TO PSYCHOLOGY

THE contributions of Darwin to psychology have not been adequately recognized. Not only in his famous seventh chapter on "Instinct" in the *Origin of Species;* in the second and third in the *Descent of Man,* comparing the psychic powers of men and animals; in his *Expressions of Emotions,* and in *Domestication,* but sometimes in other works, he not only showed a depth of insight into, but laid anew the foundations of, genetic as well as comparative psychology. These should, and I believe will, eventually make him regarded as hardly less the founder of a new departure in this field than in that of classification, form, and structure. For him the soul of man is no whit less the offspring of that of animals than is his body. Our psychic powers are new dispensations of theirs. The ascending series of gradations is no more broken for the psyche than for the soma. The gaps are no wider or more numerous from the lowest to the highest in the one than in the other. The affinities and analogies are as close, and the soul in-

herits as much from our venerable, brute forbears as does the body. The rudiments are as numerous and, to those who can rightly interpret them, as significant. From the higher anthropoids, we need to go down the evolutionary stage but a little way to span an interval quite as great as that separating even the existing great apes from the lowest savages.

But Darwin's method is always and everywhere objective and observational, never subjective or introspective. Few who have ever written about the mind of man know or say so little about consciousness, which has spun its Merlin spell of enchantment about our craft and all its works and ways. His language is the concrete facts of life and mind, and not the categories and intuitions that an ingrowing intellect loves to manipulate. The brute soul explains that of man, rather more than man explains the brute; the unconscious explains the conscious and not conversely. He posits a natural history rather than a philosophy of mind. As Steinthal said language could be studied only historically—" Sie ist was sie geworden "—so for Darwin the true, ultimate knowledge of our psyche is the description of all developmental stages from the amœba up; and those move most surely among the altitudes who have most carefully explored the depths in which the highest human powers originate. Emotions are best studied in their outward expressions in gesture, will is investi-

gated by the study of behavior, intelligence by massed instances of sagacity, and not by analysis under old rubrics. While he would have welcomed all the illuminating experiments and tests under controlled conditions, which have lately given us such a wealth of insight, he would probably have preferred careful observations of animals afield in their accustomed habitat. Let us psychologists find in this celebration motivation to re-read his masterful contributions to our science, for nothing in our perhaps all too copious literature so grows upon the mind by frequent reperusal; and thus only shall we profit to the full, as we have been tardier than the biologists in doing, by the method, direction, and inspiration he so abundantly offers us.

GENETIC SYNTHESIS THE NEED OF MODERN PSYCHOLOGY

Probably most psychologists in our day accept evolution in a general way and have only praise for Darwin; yet I can think of but very few whose interest in the studies of the soul is predominately evolutionary or very much influenced even by Herbert Spencer. Students of instinct have profited most here, although many of their studies are made under artificial and highly-specialized aspects, with too little reference to life history and habits of the species in the state of nature. The human mind is, for the most part, now studied introspectively, not only by the

literary psychologists but in the laboratory, which is more and more regarded as a method and microscope of subjective analysis. Even Wundt approached psychology from the standpoint of physics and physiology, and his great text-book would have been but very little different had Darwin never lived. The doctrine of apperception and even of feeling, with its recent, labored, introspective discussions of peripheral versus central origin and tri-dimensional theories, very rarely considers any developmental aspects; and this is one reason why, as has lately been so ably pointed out, neither Wundt nor the other standard text-books offer any aid to the student of abnormal psychology or of instinct.

Meanwhile, our science has had a prodigious and sudden horizontal expansion far beyond the old themes and limits. We have a psychology of religion, with a more special literature on such subjects as conversion, atonement, faith, possession, holy spirit, inspiration, immortality, prophecy, prayer, Sabbath, and even the process of dying, sin, and demonology. Then there is the new psychology of crime, under its special rubrics, murder, theft, arson, rape, suicide, fraud, and swindling, with traits of the chief classes of criminals. Hypnotism and suggestion, not to mention ghosts and telepathy, have opened another field. Then we have the psychology of sex in its normal and morbid manifestations, psychic differences, eugenics, and moral prophy-

laxis. There is the psychology of language, gesture, music, imitation, social instincts, truthfulness, infancy, childhood, adolescence, pedagogy, property, play, genius, and prodigies, sleight-of-hand, advertising, war, second breath, leadership, provincialism, business and panic, psychic epidemics, and many more, not to speak of the long list of admirable studies of exceptional individuals from Helen Keller to Miss Beauchamp, Flournoy's Mlle. Smith, Beers, Monod, and Mrs. Piper. Instead of restricting himself to the classic, old themes of memory, association, logic, freedom of the will, conscience, in more or less academic seclusion and aloofness, the modern psychologist is often consulted by parents, pedagogues, lawyers, legislative committees; lectures before popular audiences; or writes books and articles in a catchy, impressionistic style, with great attention to phrase-making.

Thus, present themes are so absorbing, so many and so new, that if we are not beginning to lose sight of each other, we have lacked time and incentive to keep posted and interested all over the field, until now the task has grown beyond the ability of any one less gifted than Darwin to master details, see perspective, and mosaic items into true, evolutionary order which can alone bring unity into this teeming but now chaotic domain. The material for perhaps the most majestic structure yet reared by science is already quarried. The need of and call for a master builder in this

field must, ere long, produce the man. Some of us are already convinced that the human soul in all its power is just as much a product of evolution as the body; but our faith needs to add the knowledge that can only come when all the authentic data are properly grouped. That the impending synthesis must be genetic, not in the prolix and platitudinous sense of Spencer, but with concrete facts as warp and woof, is inevitable if the psychology of the future is to correlate the facts of instinct, of daily human life with all its hot and intense impulses and all its morbid manifestations, and so become the Bible of the soul of man, in a sense our current, fragmentary systems do not dream of—this seems to me to be self-evident.

RUDIMENTARY PSYCHOSES

The signs and foregleams of such a reconstruction and transvolution are already many. In abnormal psychology, devolution is a rubric of increasing dominance. The Jacksonian theory of epilepsy brings in the genetic perspective in its conceptions of higher and lower levels. The studies of sex perversions are replete with references to the past history of the race, and some of them can be explained only as reversions, as in the case of the impulsions to nudity and exhibitionism. Many of the psychic facts in human courtship point directly to that of animals. Some of the laws of the long-circuiting of the

genesic instinct into secondary sex qualities are the same for brute and man. The more we know of this instinct the more orderly and unbroken becomes the progression upward and the closer the parallel. Even the differences are more and more explicable. The same is true of the care of the young, where the basal phenomena are common to all the higher mammals, and some of them to all viviparous creatures. Again, the correspondences between adolescence and senescence are, in some cardinal points, strangely complementary. Here, too, should be mentioned the striking morphological, pathological, and psychic indications from the study of childhood that puberty once came much earlier in our forbears, the autogenetic inferences in this direction, however, being as yet too slightly supported by phyletic facts, on account of the necessary imperfections of the record. Perhaps best of all as an illustration is the new psychology of crime and criminals, who are so shot through, body and soul, with atavisms that only the early history of the race can explain them.

Again, if we eliminate from the later studies of mental diseases, all the evolutionary elements and suggestions, they would be robbed of no little value. I refer especially to psychasthenic and dissolutive states, to certain of the phobias, fuges, imperative ideas, to various eruptive or fulminating phenomena and psycholeptic crises, and to the formation of the more or less subconscious con-

stellations of psychic elements, which may act like foreign bodies in the soul, and some of which are peculiarly suggestive of atavistic or outgrown states. Here, too, belong many phenomena of hypnoidization with more or less psychic decapitation—Verdichtung—(which probably represents a type of psychoses that are peculiarly characteristic of prehistoric man, who ejected his subjective states much as Freud thinks that dreamers are doing, to say nothing of the latest studies of phonisms, photisms, and coenesthesias. It is studies in this field, it may also be mentioned, that have led acute minds, like Bleuler, to violent polemics against consciousness as the muse of modern psychology, some of them insisting that but little of the experience that has made the mind in its human form has been connected with either consciousness, apperception, or even attention. The view is unquestionably gaining ground that consciousness is an epiphenomenon of mind, and that its function is essentially no less remedial or cathartic than the church has held confession to be, though in a somewhat different way. There is no better test of a psychological system than its applicability to psychiatry; and it is here that Wundt so signally fails, for his fundamental assumption is that consciousness is the condition of all psychic experience, and he defines even feeling as a "subjective reaction of consciousness." In fact, on the contrary, there are incessant and manifold affective and

other processes going on in us that lack consciousness, although they often resemble it in themselves and in their influence upon us, and which can not be ignored because they often dominate psychopathic symptoms and also our normal lives. These are processes which become conscious only when associated with the ego-complex. Many sudden choices, movements, feelings of anger and fear, and many other experiences sometimes lack all intellectual motivation as much as do melodic haunts. It is such states and activities, possibly mediated by sub-cortical areas, that irresistibly suggest past evolutionary stages of mentation, and it is also this group of underlying processes that may put on and off successive, conscious personalities as garments. It is these deep yet dominant complexes that love, hate, shape many currents of conduct, before consciousness is aware of it, and which are constantly reinforcing and approving or censuring what consciousness does. They suffer or rejoice sometimes with, sometimes without, consciousness, which is only their very imperfect instrument. Perhaps nothing is ever fully conscious, while much that takes place in us may be wholly unconscious. To say with Raimann that "there is no unconscious knowledge"; or with Hellpach that "psychology deals only with consciousness," and that "the unconscious can not be an object of knowledge," is a form of psycho-physic parallelism that amounts to obscurantism; while to urge, as we

must, that even attention may be unconscious would shock even an alienist so speculative as Ziehen, who persistently identifies the psychic with the conscious.

PSYCHIC "RECAPITULATION"

Hardly less than animal instinct, child psychology, as Darwin in his famous observations on infancy, although not the first was perhaps the third to see, can only be explained on an evolutionary basis. The child, uncivilized and to some extent even savage, is precociously thrust into an environment saturated with adult influences because of language and accumulated grown-up customs, traditions, and ideas; and for this reason as well as because of its intense, imitative propensities tends to be very early stripped of many of its psychic rudiments and recapitulatory traces. Yet the more we know the child, the more clearly do we see the germs of many atavistic tendencies nipped in the bud, though many of them have so long been. There can no longer be any doubt that the human infant not only tends to but occasionally does develop real words that are its own original creation, products of the rudiment of the same instinct in which language took its first rise. This vestige is thus not completely eliminated by the early, mimetic adoption of the speech of the environment. I have collected from the literature over two score of these

words which, I believe, can not possibly be explained as imitations, and which have been used consistently by the child for some time and occasionally for a number of years. So in infantile drawing we have undoubted, though dwindling, traces of what Verworn calls the physioplastic stage of paleolithic man, before the idioplastic stage of the neolith, who ceased to draw directly from the object itself but rather copied his own mental image of it. Here, again, a well-recognized phyletic stage has dwindled to little more than a filmy vestige in the modern infant, but is as recognizable as the rudimentary gill-slits in the embryo. The swimming, paddling movements, too, by new-born infants if supported in tepid water; the wonderful power to cling and support the weight for a minute or two during the first few weeks after birth, a power soon lost but reminscent of arboreal life; the phobias of infants of a few weeks or months seen often in nervous shudders at the first impressions of fur, big teeth and eyes; the joy experienced by tossing and other levitation movements, creeping, and the processes of assuming the erect position; the very intricate and interesting stages of the progressive acquirement of the complex sense of self; the loud cry of the human infant from birth on as contrasted with the silence of the new-born of other animals, so eloquent of the early power of the parent to protect; and for older children fetishisms galore, gangs corresponding to the

primitive tribes, propensity for hunting, killing, striking with clubs, pounding, stealing, etc., the sense of the power of the point, edge, string, and many forms of plays and toys, the nascent sense of death, and other items far too numerous to even catalogue here—all show that the child is vastly more ancient than the man, and that adulthood is comparatively a novel structure built upon very antique foundations. The child is not so much the father of the man as his very venerable and, in his early stages, half-anthropoid ancestor. There can no longer be any question that its rudimentary psychic organs are no whit less numerous than the half-score of anatomical rudiments that Wiedersheim enumerates. Perhaps, in general, the traces of the psychic recapitulation of the history of the race are most traceable and most unbroken, faint as some of the traces are. Psycho-genesis, like embryology, shows many rudiments preserved and developed by being diverted to other than their original uses, although of very few psychic traits or functions have there been adequate material methods of record and preservation as structural details are preserved; nevertheless, they follow the same lapidary law and speak a language which, when it is set down and interpreted, is no less clear and certain.

In general, nearly every act, sensation, feeling, will, and thought of the young child tends to be paleopsychic just in proportion as the child

is let alone or isolated from the influence of grown-ups, whose presence always tends to the elimination of these archaic elements, and in all cases makes havoc with them, over-repressing some that should have their brief fling, if only on the principle of the Aristotelian catharsis, to give early immunity from the hypertrophy of bestial traits by awakening the next higher powers that repress them in their nascent period; but which, in some environments, are left to grow into faults and then into juvenile crimes, which they are prone to do just in proportion as the order of their nascency is perverted. Thus the problem of a true mentally, esthetically and morally orthopedic education still gropes in the trial and error stage, although not without some progress toward a scientific basis for pedagogy which, if it ever comes, can rest on no other foundation than a well-established embryology of the soul, all the way from eugenics and the psychic states and regimen of pregnancy on to the fully matured nubility of the offspring. Thus, from one point of view, infancy, childhood, and youth are three bunches of keys to unlock the past history of the race. Many of the keys, especially those which belong to the oldest bunch, are lost and others are in all stages of rust and decay. Many of the phyletic locks which they fit are also lost or broken; both locks and keys are often distorted and, to change the figure, the sequences which the race followed are often inverted in the

autogenetic processional of growth; but, if the goal is still dim and far, it is unmistakable, and as we slowly and surely approach it, the genetic psychologist feels it beckoning, calling, and inspiring, almost like a new muse. This has introduced a temporal perspective or new dimension into a field where most preceding and even present studies have all been in the flat surface of the present state of adult consciousness. This is supported by, though still but very imperfectly correlated with, the studies of animal instinct on the one hand, and with those of the myth, custom, and belief of primitive races on the other. It already suggests to the many laboratory studies of the affective life (based on the method of controlling the conditions of very slight variations of emotional tone exigously made and based only on a few adult experts), a more excellent way, which would tend to bring psychology back to the study of human life as it is lived out, where it is hottest, most intense and passional with love, anger, fear, hate, jealousy, grim and dour struggles with sin, wrought out with sweat, blood, and supreme effort, with perhaps the life and death of the individual or even the race at stake. Here, rather than in the isolation of the laboratory or the study, lies the heart of a psychology that touches life and that really avails and has worth and value, because it is in line with the eternal powers and is, in a word, a true, natural history of the soul, and can make " philosophy " again, as

the motto of one of our best-known culture fraternities has it, "the guide of life."

THE PSYCHOLOGY OF THE FUTURE

Finally, education, now perhaps the most universal and uniform of all the social institutions, is now looking to psychology for guidance as never before, and we are at present able to meet this call in only a halting and partial way. Religion seems of late to be becoming strangely docile to all the too little we have to teach it. Psychiatry, to which we should have at least given a science of normal psychic life, is now in danger of finding our texts of little avail in solving its problems, is building new foundations of its own, and growing weary of our sophistic subtleties concerning parallelism and interaction and the nature of feeling, conscience, etc. Few, even of our recent experimental results, are available for determining or influencing normality or abnormality; our discussions of freedom, necessity, or responsibility are too academic for use in criminology. The great newly discovered continent of the unconscious is still regarded by many members of our guild as mystical, perhaps superliminal, and its phenomena are used to cast auguries as to whether the soul is independent of or survives the body. The unconscious is really like the submerged eight-ninths of an iceberg, which is impelled by deeper currents in a denser medium, and which the glittering summits that

emerge above the tide and are impelled by only atmospheric pressure have little control over. And once more, just as psychiatry is now changing its emphasis from a predominantly somatic and neurological basis, which has been so fruitful under the old slogan of Virchow, "Ubi est morbus," to a more psychic, pathological viewpoint, so perhaps even the doctrine of heredity is coming our way by changing the terms applied to its elements from the mystic, pathological ids and determinations of Weismann to Semon's no less mystic but psychological postulates of mnemes and engrams. Here, too, we are hardly ready to meet the new demands or utilize the new principles, because our department is still, despite its great, recent progress, only half scientific and is not unlike Milton's new-born tawny lion pawing to get away from the metaphysical and theological soil from which it sprang. We have too long yielded to the seductions of the heterai of the ancient, speculative problems that have obsessed us and not yet definitely broken with those in our midst who still urge that psychology should be developed in the closest rapport with, if not under the influence of, a speculative philosophy.

Finally, as Darwin freed biology from the inveterate dominance of the ideas of fixed and divinely created species, conceptions directly inherited from Plato's ideas and Aristotle's categories, so everything in the present psychological

situation cries out for a new Darwin of the mind, who shall break the persistent spell of theoretical problems incapable of scientific solution, the ideal of a logical and methodical exactness greater than our subject in its present stage permits of, which Aristotle well dubbed pedantry, and remand the haunting problem of the ultimate nature of consciousness and the final goal of the psyche to the same limbo, by suspending convictions, as those of the constitution or cause of energy and the nature of reality and objectivity. Only by so doing can we again get up against the essential facts of life as it is lived out by the toiling, struggling men, women, and children, normal and defective, of our day. If this rough diagnosis of the present situation is correct, only a pessimist can doubt that the need will, ere long, bring the man or the men to meet it in the only way it can be met, viz., by a comprehensive evolutionary synthesis in the psychological domain, which by every token seems at present to impend.

INDEX

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NOV 9 1977

NOV 1 [illegible] 1977

NOV 13 1978

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